ALPINE PLANT RESPONSES TO NATURAL TEMPERATURE VARIATION AND EXPERIMENTAL WARMING TREATMENTS IN SOUTHERN YUKON

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ABSTRACT

Global climate models predict that the current trend of warming in the Arctic will continue over the next century. The productivity of arctic plants is often limited by short growing seasons with relatively low temperatures such that a warmer climate could have large impacts on plants and plant communities. This study characterised alpine plant responses to changes in temperature at an alpine tundra site near Whitehorse, Yukon, Canada. I examined relationships between plant productivity and natural temperature variations and assessed responses of plants exposed to an experimental warming treatment. Non-destructive measurements of reproductive and growth characteristics of four target species (*Dryas octopetala, Lupinus arcticus, Polygonum viviparum,* and *Salix arctica*) were taken annually from 1999 to 2008. There was no significant effect of the warming treatment (OTCs) on average daily mean temperatures as midday warming of up to 1.4 °C was largely offset by night time cooling in the OTCs. Vegetative measurements of target species showed no significant responses to OTC treatments. However, peduncles of *D. octopetala* and sections of *P. viviparum* inflorescences that produced bulbils were an average of 34.6 % and 64.7 % longer in OTCs than in controls, respectively. These treatment responses were likely due to plants responding to a factor other than temperature that was modified by the chamber. One vegetative and five reproductive characteristics were significantly related to annual variation in temperature. The summer of 2004 was exceptionally hot, and some species that did not respond to smaller fluctuations in temperature showed large changes in growth or reproduction in this year, perhaps indicating a non-linear response to temperature. Among the larger responses to the warm summer of 2004 was a shift in *P. viviparum* allocation from predominantly asexual to sexual means of reproduction. Measurements of plant community composition assessed at five-year intervals showed no differences in community composition between experimental plots and controls, and changes in composition over the study period were

not uni-directional. In general, both individual plants and community composition were highly resilient to observed variation in summer temperatures. Other factors, such as nutrient availability, may be more important in determining plant responses to environmental change at this site than the direct effects of summer temperature variation.

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1.0 INTRODUCTION

1.1 Climate warming in the Arctic

It is now widely accepted that anthropogenic activities are having a profound impact on the earth's climate. In 2007, the Intergovernmental Panel on Climate Change stated with "very high confidence that the ... net effect of human activities since 1750 has been one of warming" (IPCC 2007). Global mean annual temperatures have been increasing by approximately 0.13 °C per decade over the last 50 years (Forster et al. 2007); however, the magnitude of increase is not uniform across the globe. In the Arctic, mean annual temperatures increased by 0.40 °C per decade between 1966 and 2003, with rates of up to 2 °C per decade in some regions (McBean et al. 2004). Using paleoclimate records, Overpeck et al. (1997) have reported that Arctic temperatures in the 20th century were the highest they had been in the preceding 400 years.

Tundra ecosystems are important in relation to the rise in atmospheric CO_2 as they contain large amounts of carbon (Oechel and Billings 1992) that can be lost or sequestered through various processes. The Arctic is particularly sensitive to climate warming because of positive feedbacks related to soil temperature, carbon balance, and land-atmosphere energy exchange. Increases in soil temperatures and soil drying stimulate CO_2 loss to the atmosphere (Oechel et al. 2000) and contribute to the greenhouse effect. Shifts in the balance between photosynthesis and respiration of plants could have major impacts on the flow of carbon between ecosystems and the atmosphere (Oechel et al. 1993, 2000). Increased shrub cover, which has been reported in the Arctic (Sturm et al. 2001, Wilson and Nilsson 2009), may contribute to increased snow depth in winter and lead to warmer soil temperatures. Further warming may occur if shrub stems are tall and rigid enough to be above the snow, causing a decrease in winter albedo (Sturm et al. 2005). Changes from herbaceous- to woody-dominated tundra systems may increase summer carbon

sequestration potentially buffering some of the increased carbon loss from soil warming. Rapid warming in the Arctic and the sensitivity of tundra ecosystems to higher temperatures makes it important to understand and be able to better predict responses of tundra communities to temperature changes.

1.2 Plant responses to temperature

Plants growing in arctic and alpine habitats endure harsh environmental conditions. They must contend with low summer and winter temperatures, short growing seasons, strong winds, low precipitation, and low nutrients (Savile 1972, Billings 1987). Plants have a variety of mechanisms that allow them to grow and reproduce in such environments. Examples include heliotropism (Kjellberg et al. 1982) and forming dense mats (Savile 1972) to increase tissue temperatures, and perennial growth (Billings 1974) and initiating leaves and flowers in the year(s) before emergence (preformation; Bliss 1962, Billings and Mooney 1968, Diggle 1997) to increase development time where growing seasons are short.

While arctic and alpine plants are adapted to cold temperatures, in general they are still living below their temperature optima (Tieszen et al. 1981) and even small increases in temperature can yield significant increases in growth and reproduction. Common responses to increased temperatures are advances in phenological events (Arft et al. 1999, Stenström and Jónsdóttir 2006), increases in growth and reproduction of individual species (Chapin and Shaver 1985b, Arft et al. 1999, Kudernatsch et al. 2008), and changes in community composition (Jónsdóttir et al. 2005b, Walker et al. 2006, Wilson and Nilsson 2009).

Plants in arctic and alpine environments are often limited by nutrient availability and moisture, in addition to temperature (Billings 1987, Körner 2003). Effects of increased

temperature on plant growth may be less than expected because another resource is limiting (Dormann and Woodin 2002). Temperature can also generate plant responses indirectly, via its influence on other environmental factors. For example, warmer temperatures increase the amount of nutrients available to plants by increasing rates of decomposition and nitrogen mineralisation (Hobbie 1996, Nadelhoffer et al. 1997) which in turn leads to increased plant growth (Chapin et al. 1995). Similarly, warming may decrease soil moisture through increased evaporation, which, for example, may have a negative influence on a species of moss that otherwise shows a positive response to warming (Jägerbrand et al. 2003). Temperature also interacts with biotic factors to further complicate responses. Decreases in lichens and mosses under warmer conditions are often attributed to increased competition from canopy species and not directly to increased temperatures (Cornelissen et al. 2001, Hollister et al. 2005b). Shaver et al. (2000) identify that one of the greatest obstacles in understanding responses to temperature is in the complex network of indirect effects from interactions among environmental factors and species.

Species respond individualistically to environmental conditions (Chapin and Shaver 1985b), but understanding and predicting ecosystem responses to temperature can rapidly become too daunting a task if all species in a community are considered. Chapin et al. (1996) suggested that plant growth forms are useful in describing plant responses to environmental change because species within them exhibit similar responses to environmental perturbations and have similar effects on ecological processes. Species within a growth form are not as consistent in their responses to temperature as they are in their responses to other environmental variables (e.g. water and nutrients) (Chapin et al. 1995, Chapin and Shaver 1996, Dormann and Woodin 2002), but some generalisations are possible. Deciduous shrubs and graminoids are often most sensitive to increases in temperature (Chapin et al. 1995, Walker et al. 2006), while growth responses of forbs and evergreen shrubs are generally less consistent between studies (Chapin et al. 1995, Arft

et al. 1999, Dormann and Woodin 2002). In terms of growth forms influencing ecological processes, it has been shown that woody plants negatively affect decomposition and nutrient cycling compared to herbaceous plants because wood takes longer to decompose (Hobbie 1996).

Differences in responses to temperature between species or growth forms will cause changes to the composition of plant communities. Increases in shrub cover are already being observed across arctic and alpine sites (Sturm et al. 2001, Wilson and Nilsson 2009) and in response to experimental warming (Jónsdóttir et al. 2005b, Walker et al. 2006). Decreases in species diversity have been reported in response to experimental warming as increased shrub dominance causes lower-canopy species abundance to decline (Hollister et al. 2005b, Walker et al. 2006).

1.3 Approaches to climate change research

Field-based climate change studies usually employ one of two approaches: 1) experimental studies involving the manipulation of at least one climatic variable of interest (e.g., Hollister et al. 2005b, Jónsdóttir et al. 2005b), or 2) studies based on natural spatial or temporal gradients (e.g., Walker et al. 1994, Trivendi et al. 2007). Each approach has unique strengths and limitations.

Manipulation studies provide the researcher with more control over the amount of change occurring (Dunne et al. 2004), although the extent of control varies with the type of manipulation used. Studies of this type may also be appealing for their ability to generate responses in a short time. However, interpretation of results may be hindered by unintentional experimental effects, and initial responses rarely reflecting those occurring over a longer term (Chapin et al. 1995, Arft et al. 1999, Hollister et al. 2005b). Furthermore, manipulation studies impose a sudden change to the environment that may not be representative of gradual, natural changes (Phoenix and Lee 2004).

Gradient studies often yield a better understanding of longer term responses to environmental changes (Dunne et al. 2004). Methods based on temporal gradients involve annual or semi-annual data collection from the same site to produce a multi-decadal data set (e.g., Inouye et al. 2000). This type of study provides a good indication of responses to recent climate change or climate variation, but may not yield an accurate projected response to future conditions. Results of these studies may not be easily incorporated into regional conclusions because the historical attributes of a site may have unique impacts on its present ecology (Shaver et al. 2000, Dunne et al. 2004).

Combining the use of an experimental warming treatment and temporal gradients permits assessment of species responses to directional environmental changes within the context of the range of natural variation (Dunne et al. 2004). Employing both techniques also allows the researcher to overcome some of the limitations of each method and to recognise where responses are consistent and where they are context-dependent (Dunne et al. 2004). For example, Hollister et al. (2005a) examined plant responses to experimental warming and interannual temperature variation and found that many variables responded to experimental warming, but responses were unrelated to annual variation in thawing degree days. This led them to suggest that results from manipulation alone may overestimate the importance of temperature to plants at their sites.

1.4 Thesis objectives

This study is part of the International Tundra Experiment (ITEX), which is a collaborative network of experiments carried out by scientists from more than a dozen countries working at arctic and alpine sites world-wide (Henry and Molau 1997, Molau 2001; Figure 1.1). ITEX attempts to thoroughly describe plant responses to temperature in tundra ecosystems in a variety of habitats by combining long-term monitoring of manipulated and non-manipulated plant communities, methods that are consistent across sites, and large geographical representation. It was established in 1990 in response to predictions that effects of anthropogenic climate change would occur earliest, and be greatest, at high latitudes (Henry and Molau 1997).

The study site used here has been an active ITEX site since 1998 and this study represents the first major analysis of ten years of collected data. One objective of this project was to fill a large spatial gap in the ITEX network. The study took place in southern Yukon, Canada, an area currently not represented in ITEX (Figure 1.1). This study is also one of few conducted in high-latitude alpine tundra. Plant species and communities often respond differently to temperature across sites (Graglia et al. 1997, 2001, Welker et al. 1997, Arft et al. 1999, Van Wijk et al. 2004), such that maximising geographic representation is important to understanding tundra-wide responses. Even outside the ITEX network, plant responses to temperature have been little studied in the Yukon Territory, so that this study generated results that are locally important as well as readily incorporated into the larger ITEX program. This research also contributes to a growing body of studies that combine an experimental warming treatment with monitoring responses to natural temperature variation.

The main of objective of this study was to characterise plant responses to temperature in terms of the growth and reproduction of individual species and the composition of a plant

community. Ten years of plant monitoring data were used to test for relationships between plant traits and natural, interannual variation in summer temperature. Plant responses to an experimental warming treatment were also monitored for eight consecutive growing seasons as an additional test of plant growth and reproductive responses to changes in summer temperature.

Species may be expected to respond positively to experimental warming since temperature is often limiting in arctic and alpine environments (Billings 1987, Körner 2003). Reproductive indicators have been found elsewhere to be more responsive than vegetative growth (e.g., Wookey et al. 1994, Hollister et al. 2005a), probably because of proportionally large allocation to reproduction in arctic plants (Chapin and Shaver 1985a). Deciduous shrubs may be more responsive than evergreen shrubs because of higher tissue turnover and faster growth rates (Shaver et al. 1997). In this study, I examine vegetative and reproductive responses of four target species, representing different growth forms, to an experimental warming treatment in order to assess whether there are substantial responses to temperature, and whether these responses follow patterns predicted from previous studies.

Species growth and reproduction will differ among years as plants respond to interannual variation in resources (Shaver et al. 2001). A greater number of reproductive characteristics than vegetative may be expected to respond to interannual temperature variation (Hollister et al. 2005a), similar to what has been documented for responses to experimental warming. Using a ten-year data set, I examine whether annual variation in plant growth or reproductive investment is related to interannual variation in temperature, and assess whether species responses to the experimental treatment are similar to responses to naturally warm summers.

Plant species will respond individualistically to increased temperatures (Chapin and Shaver 1985b) so I expect plant community composition to be different between experimental plots and controls. Shrub expansion appears to be one of the early responses to ongoing warming in arctic

and alpine ecosystems (Sturm et al. 2001, Wilson and Nilsson 2009) so that species such as *Betula nana* and *Salix arctica* will be more abundant in experimental plots. Lower canopy species such as lichens and mosses may be less abundant in treated plots as a result of increased shading from taller species. Species richness may be lower in experimental plots compared to controls because species will be lost quicker than new ones can colonise in response to the disturbance (Forbes et al. 2001). Using plant community data collected at five-year intervals, I assess whether community composition is different between experimental plots and controls, and whether differences between treatment types increase after ten years of exposure to the experimental warming treatment.

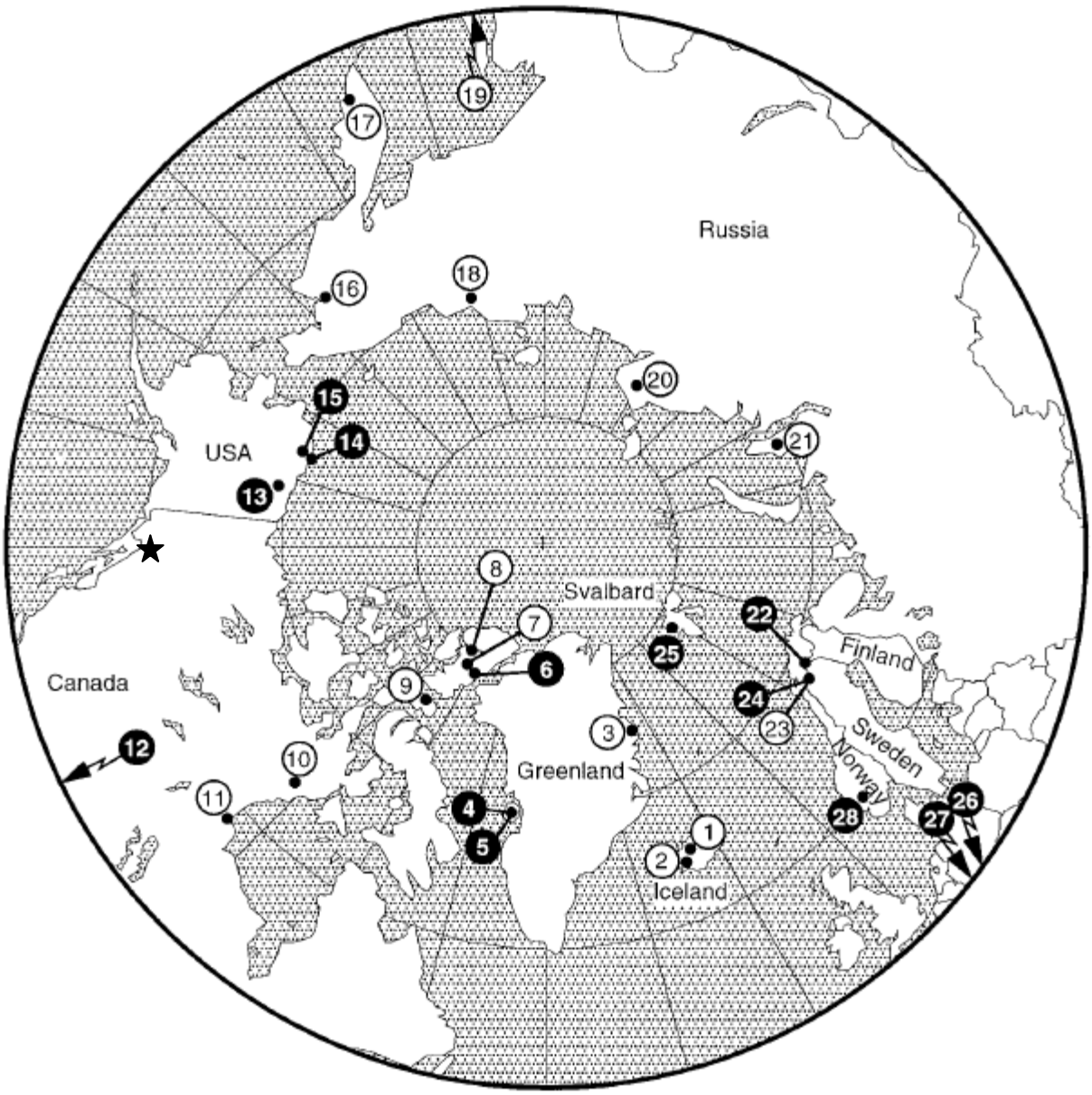

Figure 1.1: A map of research sites (numbers) for the International Tundra Experiment (ITEX). The Wolf Creek study site, near Whitehorse, Yukon, Canada is indicated with a star. Solid circles indicate study sites used in a previous meta-analysis of ITEX data. Map modified and used with permission from Arft et al. (1999).

2.0 METHODS

2.1 Study area

The study site (60° 33'47"N, 135° 07'51"W; 1526 m a.s.l.) was located in alpine tundra within the alpine zone of the Wolf Creek drainage basin and is approximately 15 km south of Whitehorse, Yukon, Canada. The Wolf Creek basin lies within the Boreal Cordillera ecozone (Yukon Ecoregions Working Group 2004).

The geologic makeup of the area is primarily sedimentary rock, made up mostly of limestone, sandstone, and siltstone (Janowicz 1999). The area is overlain with a mantle of till whose deposits are glacial, glaciofluvial, and glaciolacustrine in origin, and are anywhere from a few cm to 2 m thick (Janowicz 1999). Soils range from sandy loam to gravelly sandy loam, and incorporate a 2 cm thick layer of volcanic ash approximately 10 cm below the surface (Rostad et al. 1977). Soils at the site are Brunisolic (Clayton and Marshall 1972) and fairly mesic with a large gravel and rock component with a 3 to 5 cm deep organic layer in vegetated areas. Unvegetated areas have little to no humus development. The site is in the zone of sporadic/discontinuous permafrost meaning that the area has 10 to 50% permafrost coverage (Brown et al. 2001).

The site experiences a sub-arctic climate characterised by large seasonal variations in temperature, low precipitation, and low relative humidity (Wahl et al. 1987). The mean annual temperature is -3 °C with monthly mean temperatures of 5 to 15 °C in the summer and -20 to -10 °C in the winter (Janowicz 1999). The area receives 300 to 400 mm of precipitation annually with approximately 40% falling as snow. The site is covered with snow for seven to eight months each year. It is also quite windswept with wind speeds reaching up to 5.5 m/s and a mean monthly speed of 3.7 m/s (N. Hedstrom, R. Granger, D. Bayne and R. Janowicz, *unpublished*

data). The area receives approximately 18 hours of natural light per day during the summer months and six hours per day in the winter.

The site vegetation is characteristic of dwarf-shrub heath tundra (Bliss and Matveyeva 1992). Common plant species include mat-forming shrubs such as *Dryas octopetala*, *Salix arctica,* and *S. reticulata*, the forb *Lupinus arcticus*, graminoids (e.g. *Carex* spp., *Festuca* spp.), lichens, and mosses. There are frequent bare areas at the site caused by cryoturbation in frost boils. The site has a south-southeast aspect and a gentle slope (estimated at 1 to 3°).

2.2 Experimental setup

The project was initiated in 1998. The experimental design included two treatments: temperature manipulation using open-topped chambers (OTCs), and non-manipulated controls. The first three years of the study involved initial plant monitoring and a trial run with an alternative type of experimental chamber that had vertical sides. After these three years, temperature increases were not apparent in the treated plots relative to the controls, and in 2001 the original greenhouses were replaced with an OTC design similar to the truncated cones used in ITEX (Figure 2.1; Marion 1996). Since annual monitoring of control plots began in 1999, data on plant responses to annual variation in temperature included those from 1999 to 2008 while results of the OTC experiment were based on data from 2001 to 2008.

These OTCs had walls 40 cm tall and angled 60° to the ground, an inside basal area of 1.72 m^2, and a top opening of 0.85 m^2. Chambers were made of clear vinyl stapled onto a wooden frame with flexible plastic pipe rings at the top and bottom. There were gaps of up to approximately 10 cm between the bottom of the OTC frame and the ground surface depending on microtopography. OTCs were placed on the experimental plots for the duration of the growing

season (late May to early September) each year from 2001 to 2008. Open-topped chambers typically increase the daily mean surface temperatures by 1 to 4 °C in the summer months (e.g., Marion et al. 1997, Walker et al. 1999, Hollister and Webber 2000, Jónsdóttir et al. 2005b), although under optimal conditions increases of > 5 ºC above ambient have been recorded (Marion et al. 1997). Uncommonly night time temperatures within OTCs have been lower than ambient (Gugerli and Bauert 2001, Stenström and Jónsdóttir 2006), decreasing the amount of mean daily warming.

Study plots were laid out in a randomised block design, where 20 plots were arranged in five blocks with two replicates of each treatment per block (Figure 2.2). The effect of the slight slope at the site was not known at the outset of the experiment and blocks were arranged parallel to the slope contours to account for potential slope effects. Plots of 1 m x 1 m were permanently marked with metal stakes and spaced approximately 8 to 10 m apart. Plots were smaller than the inside area of the OTCs to minimise study plants being subject to edge effects of the chambers.

Temperature was recorded hourly in eight plots (four of each treatment type; Figure 2.2) using thermistors attached to data loggers (HOBO® 4-Channel External Input, Onset Computer Corporation, Massachusetts, USA). The monitored plots were chosen randomly once stratified by block and treatment type. Thermistors were positioned in pairs, with one measuring air temperature 5 cm above the ground surface, and the other measuring soil temperature 5 cm below the ground surface. Pairs were installed on each of the north and south sides of the plots for a total of four thermistors in each monitored plot. Above-ground thermistors were placed horizontally to the ground surface. They were shielded from direct sunlight by white PVC tubes covered with reflective material and open at each end to allow air flow. Temperatures were recorded hourly every day from July 1998 until September 2008, although technical problems caused gaps in the record.

This project was established by Yukon Territorial Government Department of Environment, and Environment Canada. Researchers within these organisations designed the study and collected data until 2007. My role in this study was to collect all 2008 data and carry out the first major analysis of the ten year data set.

2.3 Target species: descriptions and measurements

This study targeted four species for repeated, non-destructive measurements of growth and reproduction: *Dryas octopetala* L. (mountain aven, a dwarf shrub), *Polygonum viviparum* L. (syn. *Bistorta vivipara* (L.) S.F. Gray) (alpine bistort, a forb), *Salix arctica* Pall. (arctic willow, a deciduous dwarf shrub), and *Lupinus arcticus* S. Wats. (arctic lupine, a forb). The first three species listed are identified as main target species under the ITEX protocol (Molau 1996a) and have been studied at many arctic (e.g., Wookey et al. 1995, Jones et al. 1997, Gugerli and Bauert 2001) and alpine sites (e.g., Bauert 1993, Welker et al. 1997, Totland and Nyléhn 1998). *Lupinus arcticus* is endemic to north western North America, is common throughout most of the Yukon Territory (Cody 2000), and is abundant in the Wolf Creek study area.

Dryas octopetala is a semi-evergreen, woody dwarf shrub of circumpolar distribution (Molau and Edlund 1996). It is the dominant vascular species at many arctic and alpine tundra sites (Murray 1997). Reproduction occurs via the spread of asexual ramets or through seed production (Wookey et al. 1995). Ramets emerge close together, forming dense mats. Floral buds are initiated the year before emergence (Kjellberg et al. 1982). Seeds are plumed achenes dispersed by the wind. This species typically has 'wintergreen' leaves that allow for early season carbon acquisition, growth, and reproduction (Welker et al. 1997). Leaves usually live for two years, with two to five new leaves being produced annually (Welker et al. 1993).

Polygonum viviparum is a perennial rhizomatous geophyte found in a variety of habitats throughout the North (Hultén 1968). Genets of this species are long-lived, and persist during unfavourable conditions by means of an underground corm (Callaghan and Collins 1981). Reproductive structures are situated on a terminal inflorescence with flowers occupying the topmost section and vegetative bulbils located below allowing for sexual and asexual reproduction, respectively. Plants typically produce one, rarely two, inflorescence stalks in a single season, emerging in early July. Inflorescences bearing only bulbils are quite common, but those carrying only flowers have been found rarely (Bauert 1993). While mature seeds have been found (Söyrinki 1989, Bauert 1993), sexual reproduction is thought to be quite uncommon (Law et al. 1983). Fairly high levels of genetic diversity in alpine populations do indicate that sexual reproduction is maintained at least at some sites (Bauert 1993, 1996). Each year, one to four leaves emerge and mature rapidly after snowmelt. Leaves and inflorescences of *P. viviparum* are initiated four years before emergence (Diggle 1997).

Salix arctica is a dioecious, deciduous dwarf shrub that occurs in many arctic and alpine habitats (Hultén 1968). Plants can reproduce asexually via clonal ramets, or by seed. Inflorescences are catkins that are formed the year before maturation (Molau and Edlund 1996). Female catkins have many densely packed flowers. Fertilised ovaries swell and then dehisce in mid-August releasing many tiny seeds. A wreath of fine hairs is attached to each wind-dispersed seed. Sexual reproduction is thought to be less common than asexual, but this may be because of a lack of suitable conditions for germination or seedling establishment rather than low seed production (Bell and Bliss 1980). Physiological differences between sexes have been found under natural (Dawson and Bliss 1989a, b, 1993) and manipulated conditions (Jones et al. 1997, Jones et al. 1999); therefore males and females were considered separately in this study.

Lupinus arcticus is a nitrogen-fixing, perennial herb growing in habitats from moist tundra to grassy alpine slopes to heath and woodland in north western North America (Hultén 1968). Plants grow in clonal clumps with one to several racemose inflorescences emerging from many basal leaves. Each raceme bears ten to twenty flowers that yield legumes that each contain five to ten seeds. This species is an important part of herbivore diets (Frid and Turkington 2001, Seccombe-Hett and Turkington 2008) which is the context in which it has been most often studied.

For each species, a number of specific vegetative and reproductive characteristics were measured annually from 1999 to 2008. All species-specific measurements were based on recommendations and instructions of the ITEX protocols (Molau and Edlund 1996), with the exception of *L. arcticus* which is not an ITEX species. Measurements for this species were similar to those laid out for other forbs in ITEX. Plant parts that had been grazed were noted and not included in analyses. This only applied to *P. viviparum* and there was never more than one grazed stalk in a plot in a year.

Selection, marking, and measurement of plants for annual measurement followed procedures outlined in the ITEX manual (Molau and Edlund 1996). Four ramets or clones ('plants' herein) of each of the four target species were marked in each plot. Plots were divided into quarters and the plant nearest the centre of each quarter was marked. If a quarter did not contain a certain species, another plant was selected from the quarter containing the most of that species. This second plant was located as far as possible from the one that had already been marked in that quarter. In some instances fewer than four plants of a species were present in a plot. Each selected plant was permanently marked with a numbered metal tag attached with thin metal wire that was wrapped loosely around the base of the plant.

In the years after initial plant selection, plants that had died or had been lost due to tag displacement were recorded as such and another plant was randomly selected to be marked. A random number table was used to select a corner of the plot and a diagonal distance in tens of centimetres (from 10 to 90) from the selected corner. The plant located closest to this random point was tagged and assigned a new number. The number of new plants to be tagged in a year varied by species with *D. octopetala* requiring the fewest replacements (3.33 ± 0.85 new plants per year; mean ± SE) and *P. viviparum* requiring the most (8.00 ± 1.84).

Leaf dimensions (mm) were the predominant measure used to indicate vegetative productivity of target species. For *D. octopetala* a transect line was run from the southwest corner of the plot to the tagged plant. The lengths of the five leaves closest to the tag and touching the transect line were recorded, and an average leaf length was calculated for the plant. For *L. arcticus* the longest petiole and the longest leaflet borne on it were measured. Leaf width for *P. viviparum* was measured at the widest point of the largest leaf. The number of leaves was also recorded. The longest leaf of *S. arctica* was measured, including the petiole. Annual stem increment was also measured for this species as the distance from the previous year's bud scar to the end of the terminal wintering bud (Molau and Edlund 1996).

For most species inflorescence length (mm) was used to indicate reproductive investment. The peduncle length of the *D. octopetala* flower closest to the tag and along the transect line that was laid for leaf measurement was recorded. For *L. arcticus* the number of inflorescences on the rosette was recorded. The *P. viviparum* inflorescence was divided into the section of the rachis that produced bulbils (herein 'bulbil section') and the section that produced flowers (herein 'flower section') and each was measured separately. The bulbil section was measured from the bottommost bulbil (or bulbil scar) to the bottommost flower (or to the top of the inflorescence if flowers were not present). The flower section was considered to be from the bottommost flower

to the top of the inflorescence. *Salix arctica* catkin length was measured from the subtending leaf axil to the top of the catkin. Collection of target species data was often completed after male *S. arctica* catkins had fallen off so only female catkin data were included in the analyses.

Density of reproductive structures was assessed by recording the number of inflorescences of each species flowering in a plot. This was recorded in mid- to late-July each year. Inflorescences of all flowering species, not just the target species, were included in the counts. Only female inflorescences of *Salix* species were included in the analyses of inflorescence count data.

Leaves and seeds of target species were collected in 2008 to better understand the importance to the plants of the morphological characteristics that were measured annually. Because this study was on-going, plants within plots could not be destructively sampled and collections were therefore made from plants growing at the study site, but outside the plots. Two 60 m transects were oriented in random directions within the study area. At each 2 m mark, samples were collected from the closest plant of each target species. The criteria used to select leaf samples were the same as those used in the annual measurements. For example, for *L. arcticus* the annual leaf measurement was taken using the longest leaflet on the longest petiole of the marked plant; therefore the entire leaf on the longest petiole of the closest plant was collected. Fruits of an inflorescence on the plant were collected if they were sufficiently ripe, based on the following criteria: a) seed plumes on *D. octopetala* inflorescences had opened from the initial twisted stage, b) *L. arcticus* pods were dry but still mostly unopened c) *P. viviparum* inflorescence stalks had at least one visible bulbil, and d) *S. arctica* catkins had more than one swollen ovary. Once a leaf or inflorescence was deemed appropriate for collection, measurements consistent with annual measurements were taken. In addition, the numbers of flowers and bulbils

on *P. viviparum* inflorescences were also recorded. All measurements were made while the leaf or inflorescence was still attached to the plant to best mimic the measurements made annually.

Leaves from 51 plants of each target species were collected on July 16, 2008 and processed to obtain measures of biomass and leaf area. Fresh leaves were photocopied soon after collection, and the photocopies were later used to estimate leaf area at the University of Saskatchewan using a digital scanner and the software WinFolia version 2007b (Regent Instruments Inc. 2007). Artificial 'leaves' of a known area were also photocopied and analysed with WinFolia in order to correct for any error caused by using photocopies as opposed to fresh leaves. I found a highly significant relationship ($r^2 = 0.999$; n = 5; $P < 0.001$) between area of the actual 'leaf' and that of the photocopy and used the resultant regression equation ($y = 1.02x - 0.443$) to estimate the area of fresh leaves. After being photocopied, leaves were placed in paper bags and dried at 60 ºC for 48 hours, and then dry weight was measured (mg).

Inflorescences (n = 25 to 35) of each target species were collected on August 6, 2008. Inflorescences were stored in plastic bags and refrigerated overnight following collection, and then transferred into envelopes and dried at 30 ºC for 72 hours. Once dry, inflorescences were put back into plastic bags and stored in the freezer (-18 ºC) for five to six months until they were processed.

Seeds of *D. octopetala* and *S. arctica* were assessed in terms of their viability (whether or not they contained an embryo) and germinability. No seeds of *P. viviparum* were found, but the number and mean dry weight (mg) of bulbils per inflorescence were recorded. Since pods of *L. arcticus* do not ripen simultaneously, many had already dehisced and (presumably) dispersed seeds upon collection so this species was excluded from these analyses. Dormancy-breaking techniques were not required for *D. octopetala* (Bliss 1958) or *S. arctica* seeds (Densmore and Zasada 1983), but plumes and hairs were removed, respectively.

Seeds from a single inflorescence were placed in 9 cm plastic Petri dishes on two layers of filter paper moistened with deionised water. Seeds were arranged so that they were not touching each other or the edge of the dish. Dishes were randomly arranged under fluorescent lights (18 hours light, 6 hours dark). The room was not temperature controlled, but was approximately 20 ºC. Germinated seeds were counted and removed daily. A seed was considered to have germinated when the radicle was approximately twice the length of the seed. Seeds were moistened with deionised water whenever needed. Tests were terminated when no germinated seeds were found for five consecutive days.

2.4 Community composition

Species composition was measured in each plot using a modification (Walker 1996) of the point-intercept method originally proposed by Levy and Madden (1933). While their method used points in a line to determine cover, a grid-quadrat frame method most similar to that described by Stanton (1960) was used in this study. Point-intercept techniques are among the most objective methods for determining cover and frequency of plant species in open habitats as they reduce observer bias (Crocker and Tiver 1948, Goodall 1952, Bonham 1989).

Point-frame data were collected in mid- to late-July in 1998, 2003 and 2008. A 1 m^2 quadrat was strung across with ten strings spaced equidistance apart on each of two perpendicular sides yielding 100 string intersections spaced at 10 cm intervals (Walker 1996). The quadrat was set on adjustable legs to allow it to be suspended over the plot. The quadrat was raised so that the grid was just above the height of the tallest plant in the plot. Each side of the quadrat was then levelled using a bubble level. A long pin with a diameter of 1.6 mm was lowered at each string intersection. Vegetation cover was measured by recording each live plant part that intersected the pin (called a 'hit'). Vascular plants were identified to species, while lichens and mosses were

recorded as such. Nomenclature of vascular species followed the Integrated Taxonomic Information System (ITIS 2009). It was common for a species to register >1 hit per pin drop. The numbers of hits on a species in a plot were summed to represent the species abundance in that plot. Species present in a plot, but not hit were also noted in order to increase accuracy of assessing species richness (Godínez-Alvarez et al. 2009). Species not identifiable in the field were given a pseudonym and a sample was collected for later identification. The point frame quadrat was carefully relocated on the plots each year so that differences in contacts recorded between sampling times reflected changes in community composition that occurred in the plot over time.

2.5 Data analyses

Plot-level values were used as replicates for all analyses (n = 1 to 4/treatment type for temperature data; n = 8 to 10/treatment type for target species data) and a *P*-value of 0.05 was used to assess significance. Most repeated measures analyses of variance (ANOVA) were carried out with Year as the repeated measure and Treatment as the fixed factor. Unless otherwise stated, all statistical analyses were done using SPSS Statistics version 17.0 (SPSS Inc. 2008).

2.5.1 Experimental treatment and natural temperature variation

Temperature data were first checked for possible errors and data quality issues. I considered values greater than 50 °C and lower than -20 °C to be due to technical errors, and removed them from the data set. In several cases there were large (up to 20 °C) differences between north and south temperature measurements for the same plot, but I was unable to find a pattern or determine which (if either) of the measurements was inaccurate. Once north and south temperatures were averaged into plot-level means there seemed to be little difference in hourly temperatures

between loggers within a treatment type; therefore data were left unaltered. Average daily means, minimums, and maximums were similar between loggers within a treatment type. Technical irregularities caused some data to be missing. June and July data from 2007 were missing from both treatment types and this year was not included in analyses of treatment effects. June measurements in 2001 were missing from OTCs so GDD was not reported for experimental plots in 2001. All other year-treatment type combinations had at least one logger that was complete or only missing a few (less than 5) days of measurements.

I examined temperature responses to the OTC treatment as a hierarchy of potential effects from coarse to fine levels of detail. These involved differences between treatment types in: a) average monthly mean, minimum, and maximum temperatures across all years, b) seasonal heat sums such as growing degree days across all years, c) average daily mean, minimum, and maximum temperatures in specific years, and d) average diurnal temperature patterns in specific years. I used this hierarchy of analyses because, although effects at coarse scales suggest the presence of finer scale effects, the opposite may not be true. For example, uneven increases in daily minimum and maximum temperatures have been reported in previous experimental warming studies (Marion et al. 1997, Gugerli and Bauert 2001, Stenström and Jónsdóttir 2006). These would be missed if only average monthly temperatures were analysed. Although climate models focus on mean annual or monthly patterns (Christensen et al. 2007), plants may also be responsive to changes in the diurnal (or smaller-scale) temperature fluctuations (Hollister 1998). This makes differences in diurnal patterns between treatment types important in understanding plant responses to temperature change. Analyses focused on temperature data from July, as that is the period of peak production for the plants (Johnson and Tieszen 1976) and also the time when plant measurements were made.

Plot-level hourly temperatures were averaged into daily or monthly temperatures. The effects of treatment on average monthly mean, minimum, and maximum temperatures were each assessed using two-way ANOVA with Year (2001-2006, 2008) and Treatment as fixed factors (fixed model ANOVA) (Johnstone et al. 1996). Bennington and Thayne (1994) describe fixed factors as explanatory variables for which the levels of the factor are specifically chosen by the researcher. While this is obviously the case for treatment, the classification of a measure of time into fixed or random effects is often more difficult (Searle 1971, Bennington and Thayne 1994). Eisenhart (1947) laid out three criteria for determining if a factor is fixed: 1) levels of the factor were chosen because they are of particular interest, 2) conclusions will be confined to the levels of the factor that were actually studied, and 3) the same levels of the factor could be used again if the experiment were repeated. In this study, year does not meet the third criterion, nor were the years chosen *per se*, but the effects of the individual years are of particular interest because differences in treatment effects in different years can be related to plant responses in that same year (Bennington and Thayne 1994).

Cumulative growing degree days (GDD) for each summer were also compared between treatment types. These values were calculated by subtracting a base temperature (5 °C; Molau 1996b) from the hourly air temperature and then averaging those hourly values across a full 24-hour period to get the GDD for that day. Negative hourly values were considered zero GDD. For each year GDD from June 1 to August 31 were totalled for each plot and these plot-level values were averaged by treatment type (see Figure 3.2 for sample sizes). Two-way ANOVA was used to determine the effects of treatment type and year on GDD, with each variable being entered as a fixed factor. Tukey's honestly significant difference tests (Zar 1999) were done after the ANOVAs on average July temperatures and GDD to determine which years were significantly different from one another.

In order to test for the presence of a treatment effect at a more detailed time scale (days within months), I looked at the years with the warmest (2004) and coolest (2008) mean July temperatures. For these years, I compared average daily mean, minimum, and maximum temperatures between treatment types. I used repeated measures ANOVA in order to account for potential autocorrelation among dates (Meredith and Stehman 1991, Marion et al. 1997). Treatment was a fixed factor, Day was the repeated factor, and individual plots served as replicates. Only loggers which had complete data for the month of July (2004: n = 3 control, 2 OTC; 2008: n = 3 control, 4 OTC) were used in the repeated measures model, which lead to an unbalanced data set. To best contend with this I used a Type III sums of squares (SS) as recommended for fixed models (Shaw and Mitchell-Olds 1993). This type of SS provides the most easily interpretable results when all treatment combinations are represented but the number of observations per combination differs (Speed et al. 1971). The assumption of sphericity was violated in all cases so the Huynh-Feldt adjustment (Huynh and Feldt 1976) was used to determine significance.

To examine diurnal patterns of temperatures in experimental plots relative to controls, I estimated the temperature deviation between treatment types by subtracting hourly temperatures in the control plots from hourly temperatures in the experimental plots (ΔT; °C). These hourly temperatures were mean values of all plots of a treatment type. Days in July in a given year were used as replicates (n = 31) to generate mean values for each hour in a 24-hour period. Diurnal patterns in temperature deviance were compared between the warmest (2004) and coolest (2008) summers that occurred during the study period.

To evaluate whether the efficacy of OTCs was influenced by other climatic variables such as wind speed and solar radiation (Marion et al. 1997), I used multiple regression analysis to test the impacts of climate variables on daily July ΔT. Candidate predictor variables were wind speed

(m/s), ambient temperature (°C), and cloudiness index. Wind speed and cloudiness index were obtained from the Whitehorse International Airport (herein 'Airport'; 60° 42.600' N, 135° 4.200W; 706 m a.s.l. elevation; Climate Station ID#: 2101300) (Environment Canada 2009a), located approximately 15 km northeast of the study site. Qualitative measurements of cloudiness were converted into ordinal data based on the following scale: 0 = clear, 1 = mainly clear, 2 = mostly cloudy, 3 = cloudy, 4 = fog or smoke, 5 = rain. Ambient temperature data were the above ground temperatures from the control plots at the study site. Hourly data for all variables were averaged into daily means. Multiple regression analyses were run using one of three daily measures of ΔT: the summed daily deviation, the summed midday (10:00 – 14:00 inclusive) deviation, and the summed night time (0:00 – 4:00 inclusive) deviation. These time periods were selected because they had the largest positive ΔT (greatest experimental warming) and the largest negative ΔT (greatest cooling), respectively. Analyses were run separately for four different years: 2004 and 2008 as they were the warmest and coolest years during the study period, and 2003 and 2006 as these years had the greatest positive and negative cumulative July temperature deviations, respectively. Backward stepwise elimination of variables was used to find the best regression models (Zar 1999).

Natural variation in GDD was related to annual target species measurements and densities of reproductive structures to determine the effects of GDD on the growth and reproduction of target species and community-level flowering. Plant measurements and GDD were from control plots so as to capture plant responses to natural variation in temperature. Temperature data were incomplete for 1999, 2000, and 2007. However, there was a highly significant relationship between GDD based on temperatures from the Airport and those from the study site ($r^2 = 0.927$; n = 7; $P < 0.001$) so I used the resultant regression equation ($GDD_{Wolf\ Creek} = 0.789 \times GDD_{Airport} - 212.61$) to calculate missing GDD data from the study site.

2.5.2 Plant productivity

Before proceeding with any analyses of plant variables, I tested whether there was a significant effect of blocks on plant measurements. I used one-way ANOVAs to test for differences between blocks based on pre-treatment data (1999). In instances where the variances were not equal between groups (P-value < 0.05), I used Welch's test statistic (Welch 1951) to assess significance (Levy 1978, Dijkstra and Werter 1981), though it did not change statistical conclusions. These tests revealed no effects of blocking. One measure (leaf length of male *S. arctica*) had a P-value of 0.087, but inspection of the data revealed an outlier (mean ± 2.0 SD), and when it was removed the block effect was not significant ($P = 0.309$).

To confirm the absence of a block effect, I used two-way ANOVA on 2008 target species data to test for an interaction between block and treatment type. There was a significant effect of the interaction for one measure (length of the flower section of *P. viviparum*; $P = 0.002$). However when I examined the data for this measure from other randomly selected years (2004, 2007) I found no significant effects ($P > 0.05$). I therefore concluded that blocking the plots had no significant effects on the species specific measurements and the remaining analyses were run as a completely randomised design. I also used MANOVAs to determine whether there was a significant effect of observer on measured plant variables. Observers varied year-to-year so that repeated measures analyses were not possible. Because a test of observer effects cannot assume observations made by the same observer are independent, I used MANOVAs to test for an overall effect of observer on all plant traits measured in a given year. Significant MANOVA results were followed by individual ANOVAs to assess which variables differed among observers.

I used repeated measures analyses to determine the effects of year and treatment type on annual target species measurements. Tests were carried out separately for each target species.

There were no significant differences between male and female *S. arctica* in terms of leaf length (Sex: $F = 0.001$; df = 1, 20; $P = 0.978$; Year x Sex: $F = 1.414$; df = 7, 140; $P = 0.204$; Sex x Treatment: $F = 0.192$; df = 1, 20; $P = 0.666$) or annual stem increment (Sex: $F = 0.002$; df = 1, 20; $P = 0.969$; Year x Sex: $F = 1.222$; df = 7, 140; $P = 0.295$; Sex x Treatment: $F = 0.148$; df = 1, 20; $P = 0.704$) so these data were pooled. Data rarely satisfied the assumptions of parametric statistical tests and were rank transformed prior to analyses (Conover and Iman 1981). For the most part, this did not change statistical conclusions. Multivariate analysis of variance (MANOVA) was used to account for potential correlation between variables, since, for some species, more than one measurement of growth or reproduction was taken on the same plant. There is evidence that vegetative and reproductive measurements respond differently to experimental warming (e.g., Wookey et al. 1994, Jones et al. 1997, Arft et al. 1999), so vegetative and reproductive characteristics were considered separately. Pillai's statistic (Pillai 1955) was used to assess significance. Of the four most commonly used MANOVA statistics, Pillai's has been shown to be the most robust to unequal covariance matrices and departures from multivariate normality (Olson 1974, 1976). Significant MANOVA results were followed by repeated measures ANOVA to determine which measurements were different. MANOVA was not carried out where plant variables for a species were not correlated or if only one variable was measured, and I performed ANOVA on variables separately instead (Zar 1999). For several variables the dataset was unbalanced and I used a Type III SS as in the temperature analyses.

The numbers of inflorescences of each species in a plot were standardised by dividing annual counts by the average abundance of that species measured using point intercept sampling in 1998, 2003, and 2008. This standardisation accounted for differences in inflorescence numbers due to variations in species abundance. Repeated measures ANOVAs were carried out on each of the most common species of each growth form to assess the effects of year and treatment type.

Repeated measures ANOVAs performed on absolute counts of inflorescences did not yield different results from those based on standardised counts and are not presented here. I used independent samples *t*-tests on pre-treatment data (1999) to ensure plant variables and inflorescence counts were not different between experimental and control plots before the treatment was applied in 2001.

In order to determine the effects of natural temperature variation on growth and reproduction, I used regression analyses to test for relationships between annual plant measurements and GDD. These analyses were run using plant data (target species measurements and density of reproductive structures) and GDD that were each averaged across control plots within a year. Since data were from control plots only I included data from the preliminary collections in 1999 and 2000. Inflorescence counts of some species were carried out in 1998 so data from this year were included as appropriate. Regression analyses on inflorescence counts were carried out using absolute counts and those standardised by average abundance. GDD in 2004 was abnormally high due to a very hot June so analyses were run with and without 2004 data. Analyses that excluded 2004 data allowed me to more accurately characterise species responses to typical annual variation in GDD. Comparing these results to those that included 2004 allowed me to better understand responses to a single very warm summer, the incidence of which is expected to increase with climate warming (Christensen et al. 2007). Spearman's rank correlation (Spearman 1904) was used instead of regression analysis if data violated assumptions of normality or equal variance (Zar 1999). However, using non-parametric methods did not change statistical conclusions.

I looked at bivariate correlations between other environmental variables and plant measurements in order to determine if other factors besides temperature had large influences on plant productivity. Variables included: total winter snowfall (cm, October to March), snow depth

at the end of March (cm), mean January temperature (°C), and total summer precipitation (mm, June to August). Because leaves and inflorescences are preformed in many species (Billings and Mooney 1968), I considered environmental data from the current year as well as from the previous year. GDD was included in the previous year's data. Environmental data were from the Airport (Environment Canada 2009b), except previous year's GDD, which was from the control plots.

I used regression analyses on samples collected in 2008 to determine how well variations in leaf and inflorescence morphology captured variations in leaf mass and area, and seed production and germination, respectively. These productivity measurements are likely more biologically important to the plant than the non-destructive annual measurements that were made on target species. For examples, leaf area and mass are strongly related to photosynthetic capacity and leaf nutrient levels (Wright et al. 2004), and longer peduncles of *D. octopetala* may yield heavier, more viable seeds (Welker et al. 1997). The more biologically important measurements could not be made annually due to their destructive nature.

2.5.3 Community composition

I calculated species richness, Pielou's evenness (Pielou 1966), and Shannon-Weiner diversity (Shannon 1948, Magurran 1988) for vascular plants in each plot. Indices were calculated using PC-Ord version 5.19 (McCune and Mefford 2006). I used repeated measures ANOVA to determine if there were differences in diversity measures between years and treatment type.

Data for each species were relativised by the total number of hits in a plot to remove noise from variation in total abundance and to better focus the analyses on changes in species composition of plots (Will-Wolf et al. 2006). Rare species were left in the data set. Outlier

analysis revealed one outlier plot (average Sørensen distances greater than 2.0 SD from the mean of all plots) in the data set which was removed prior to subsequent analyses. It was an experimental plot and differed from all others mainly by having almost no *D. octopetala* and a high abundance of *Betula nana*. The plot was an outlier in all three years.

To determine whether community composition changed over the study period I first calculated Sørensen distances between relative species abundance of each plot from different years, as:

$$D_{j,h} = \frac{\sum | a_{ij} - a_{hj} |}{\sum a_{ij} + \sum a_{hj}}, \quad (2.1)$$

where a_{ij} is the relative cover of species *i* in a plot in year *j* and a_{hj} is the relative cover of species *i* in the same plot in year *h* (McCune and Grace 2002). Greater values of $D_{j,h}$ indicate greater change in composition between years. I calculated distances for each of three time intervals: 1998 to 2003, 2003 to 2008, and 1998 to 2008. I performed a one-sample *t*-test on distances between 1998 and 2008 to determine if they were significantly different from zero, where zero indicates that community composition is not different between years. I used repeated measures ANOVA on calculated distances to determine if there were differences in the amount of change between time intervals and treatment types. Only the two five-year intervals were used since the ten-year interval is not mutually exclusive. Time interval was the repeated factor and Treatment was a fixed factor. A significant interaction between Interval and Treatment would indicate that composition had changed directionally more in experimental plots than in controls (Price and Waser 2000). Analyses were run separately on distance measures based on relative growth form abundance and on those based on relative species abundance.

To show the arrangement of plots based on species composition and explore patterns over time I used non-metric multidimensional scaling (NMS; Kruskal 1964). NMS is an iterative

ordination technique that positions entities based on ranked distances between plots and avoids the assumption of normality (McCune and Grace 2002). It provides the best fit of *n* entities (plots here) in *k* dimensions that minimises the stress on the final configuration (McCune and Grace 2002). The technique is often used with community data (e.g., Waichler et al. 2001, Wahren et al. 2005, Will-Wolf et al. 2006). The stress value indicates how well the distances in the associated ordination represent the distances between plots in *n*-dimensional space (McCune and Grace 2002). Stress levels of five to ten signify a good representation of the data with little risk of drawing false inferences, while levels of 10 to 20 provide a satisfactory representation with the possibility of being misled increasing with stress (Clarke 1993, McCune and Grace 2002). The ordination was run with a random starting configuration in the auto-pilot mode of PC-Ord (McCune and Mefford 2006). Two hundred fifty runs with real data were completed. A Monte Carlo test using 250 runs with randomised data was used to determine the optimal number of ordination axes and to indicate whether NMS extracted stronger axes than expected by chance. Solutions were considered stable if the final instability was less than 10^{-4} (McCune and Grace 2002).

The ordination was performed using vascular species data for all plots in all years. Several overlays increased the interpretability of the ordination. Treatment type and a joint plot of growth form types (including lichens and mosses) were overlaid to show potential differences between treatments, and show relationships between growth forms and ordination scores, respectively. Successional vectors were used to indicate whether vascular species composition changed directionally between sampling times. I calculated rank correlations (Kendall's τ) between each ordination axis and the different growth forms (McCune and Grace 2002).

Several different researchers were involved in collecting the community composition data during this study. In 2008 five plots were assessed independently by each of two observers in

order to estimate the degree of observer bias present in the data. I used a blocked multi-response permutation procedure (MRBP; Biondini et al. 1988) to determine if there were differences in composition between observers. MRBP is a non-parametric randomisation procedure to test for differences between *a priori* groups. MRBP focuses the analysis on within-block differences that are presumably due to the effect of the treatment alone (McCune and Grace 2002). The procedure generates a test statistic, the chance-corrected within group-agreement (or "effect size"; denoted A), and a P-value. The A value indicates the level of within-group homogeneity compared to what would be expected with random groupings. When all samples within a group are identical $A = 1$ and if heterogeneity within groups equals that expected then $A = 0$. It is also possible for $A < 0$ if there is less homogeneity within groups than is expected by chance (McCune and Grace 2002). MRBP was carried out using Euclidean distances (Zimmerman et al. 1985, Mielke 1991). Something to consider when performing MRBP is whether or not to align the medians within a block to zero. Alignment was not used here because McCune and Grace (2002) recommend that alignment not be used when determining an exact match between groups (observers here).

Figure 2.1: Photograph of an open topped chamber (OTC) used in the study. The design was modified from the standard ITEX design (Marion 1996). The photograph was provided by Environment Canada.

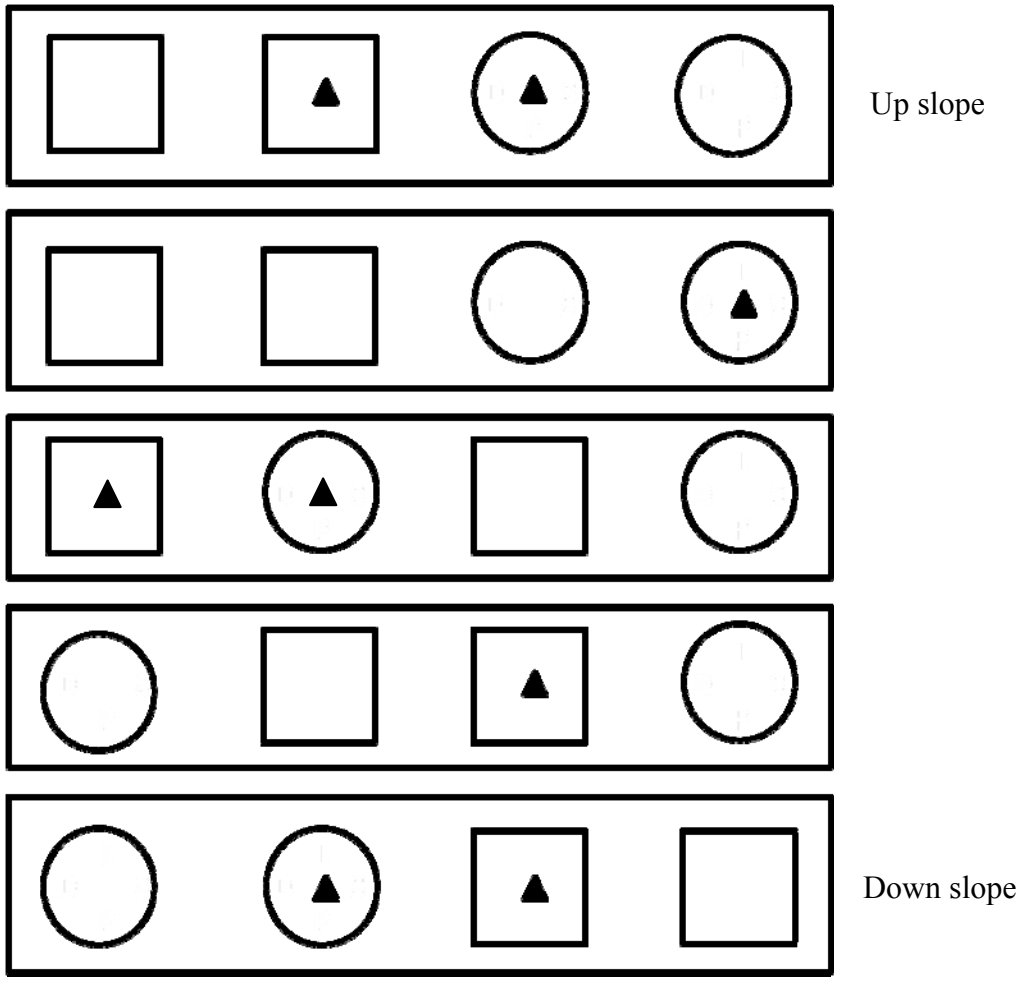

Figure 2.2: Conceptual layout of plots at the Wolf Creek study site. Large rectangles indicate the study blocks that were arranged across a slight slope. Circles represent plots with OTCs and squares denote control plots. Plots were spaced approximately 8 to 10 m apart. Solid triangles indicate plots where temperature loggers were installed. The drawing is not to scale.

3.0 RESULTS

3.1 Temperature

The OTCs had no apparent effect on average monthly temperatures observed in 2001 to 2008. Average July mean, minimum, and maximum temperatures were not significantly different between treatment types for either air or soil ($0.01 \leq F \geq 1.09$; df = 1, 30; $P > 0.05$) though differences were significant between years ($2.90 \leq F \geq 16.17$; df = 6, 30; $P < 0.05$) (Figure 3.1). While results presented are from July, average mean, minimum, and maximum temperatures from June and August showed similar patterns. Significant differences between years in air temperatures were mostly a result of temperatures in the warmest (2004) and coolest (2008) summers being different from most other years (Figure 3.1 A). Significant annual differences in soil temperatures, however, were a result of temperature in 2004 and 2008 being different from each other, while each was still similar to most other years (Figure 3.1 B).

There was no significant difference in total GDD between OTCs and controls in any year (Treatment: $F = 0.001$; df = 1, 21; $P = 0.971$; Year x Treatment: $F = 0.261$; df = 5, 21; $P = 0.929$). Differences in GDD between treatment types were suggested in the comparison of means and standard errors in some years (Figure 3.2); however these were not large or consistent enough to yield a significant treatment effect in the repeated measures ANOVA. GDD significantly differed between years ($F = 7.147$; df = 6, 21; $P < 0.001$), with 2004 having the highest GDD and 2008 the lowest (Figure 3.2). GDD at the study site in 2004 was 53% higher than the mean from 2001 to 2008. This was mainly due to very high June temperatures. The average of monthly mean June temperatures from 1971 to 2000 from the Whitehorse Airport was 11.8 °C (Environment Canada 2009a), while in 2004 it was 17.8 °C.

Temperatures measured on a daily scale revealed similar results to monthly temperatures. Repeated measures ANOVA on 2004 and 2008 data indicated that average daily mean, minimum, and maximum temperatures varied among days but were not different between treatment types for either the warmest (2004) or coolest (2008) July in the study period (Table 3.1). Interactions between day and treatment type were also not significant (Table 3.1).

Temperature patterns in OTCs compared to controls varied throughout the day, with temperature deviations being mainly positive during midday and negative at night (Figure 3.3). Average hourly air temperatures in 2004 were close to 1.5 °C warmer in experimental plots at midday, while night time temperatures showed no net warming or cooling. In 2008, average midday air temperatures showed a trend of being slightly higher in OTCs compared to controls, but these differences were not significant. However, average night time temperatures in OTCs were up to 0.9 °C cooler in 2008 compared to controls. For soil temperatures, average hourly temperatures in 2004 were higher in experimental plots than in controls during midday and late afternoon, but did not differ at night (Figure 3.3 B). Average hourly soil temperatures in 2008 were higher in control plots than in OTCs (negative deviations) for all hours, but this effect was smaller and not significant during midday (Figure 3.3 D). Relatively large fluctuations in temperature deviations (0.70 to 1.0 °C) at hours 15 and 19-20 in 2004 were unexpected, but may be due to shading of the thermistors by the OTC frame.

Multiple regression models tested the influence of climatic variables on temperature deviations (ΔT) in OTCs compared to controls (Table 3.2). Night time temperature deviations were not generally well predicted by climate variables, and models were significant only for 2003 and 2004. Cloudiness index was a significant variable in 2003 and 2006 when average temperature deviations between experimental plots and controls were greatest (Figure 3.4). When present in a model, cloudiness index and wind speed were always negatively related to ΔT.

Ambient temperature was negatively related to total and midday ΔT in 2008, but was positively related to total and night time ΔT in 2004.

3.2 Vegetative growth

Plant traits in OTC plots and controls were not significantly different ($0.021 \geq |t| \leq 2.10$; n = 6 to 10; $P > 0.10$) before the treatment was applied so that any differences between treatment types found after 2001 can be attributed to the treatment itself and not to initial conditions. This was the case for vegetative and reproductive characteristics and inflorescence counts. There were significant effects of observers in 1999, 2004, and 2005. Subsequent ANOVAs on 2005 data did not yield significant differences between observers for any individual plant trait. Two and three traits had estimates that differed between observers in 1999 and 2004, respectively. Estimates of peduncle lengths of *D. octopetala* in 1999, number of *L. arcticus* inflorescences and *S. arctica* catkin lengths in 2004, and leaf widths of *P. viviparum* in both 1999 and 2004 were significantly different between observers. However, because observers did not systematically make measurements in control or treatment plots, these occasional differences between observers are unlikely to have influenced the assessment of treatment effects.

MANOVAs were carried out on vegetative indicators of *L. arcticus* and *S. arctica* while leaf characteristics of *D. octopetala* and *P. viviparum* were assessed using ANOVA. MANOVA results showed that vegetative indicators of *S. arctica* were different between years, and that leaf characteristics were not different between treatment types for either species (Table 3.3). *Dryas octopetala, P. viviparum*, and *S. arctica* each had at least one vegetative measurement that differed significantly between years (Table 3.4). *Dryas octopetala* leaf lengths were greatest in 2007, but remained fairly constant for the rest of the study period (Figure 3.5 A). *Polygonum viviparum* leaf widths tended to increase over the study period, while the number of leaves

showed little overall pattern (Figure 3.5 C and D). *Salix arctica* leaf lengths did not differ year-to-year, but annual stem increment did (Table 3.4). Annual growth of *S. arctica* was much lower in 2001 and 2004 compared to the rest of the study period (Figure 3.5 E). While there were significant differences in growth of *S. arctica* between many pairs of years, growth in 2001 and 2004 were more than 60% lower than the average from 2001 to 2008. Leaves and annual stem increments of *S. arctica* tended to be longer in OTCs than in controls (Figure 3.5 D and E), but no vegetative measurements were significantly different between treatment types (Table 3.4).

Leaf lengths of *S. arctica* were negatively related to GDD; however the relationship was only significant when data from 2004 were excluded (Figure 3.6 D). Leaf lengths of *D. octopetala* tended to increase with GDD though trends became unclear when 2004 data were considered (Figure 3.6 A). Leaf dimensions of *P. viviparum* and *L. arcticus* and annual stem increment of *S. arctica* showed no clear trend with GDD with or without 2004 data (Figure 3.6). Despite 2004 having a much higher GDD than was average for the study period, for the most part vegetative measurements from this year were within 1 SD of the mean value for the full 10-year period. The annual stem increment of *S. arctica* was the only exception with the 2004 average more than 1.5 SD lower than the study mean.

3.3 Reproductive investment

3.3.1 Target species

ANOVAs indicated that peduncles of *D. octopetala* and bulbil sections of *P. viviparum* were significantly longer in experimental plots compared to controls (Table 3.4, Figure 3.7 A and C). There was a significant interaction between Year and Treatment for *D. octopetala* peduncle lengths (Table 3.4). Subsequent one-way ANOVAs indicated that peduncle lengths were only

significantly different between years in control plots (control: $F = 3.063$; df = 1, 18; $P = 0.007$; OTC: $F = 1.033$; df = 1, 18; $P = 0.416$), and that peduncles in treated plots were significantly longer than those in controls in 2005 (133% longer; $F = 9.597$; df = 1, 18; $P = 0.006$), 2006 (50% longer; $F = 8.427$; df = 1, 18; $P = 0.009$), and 2008 (107% longer; $F = 29.540$; df = 1, 18; $P < 0.001$) (Figure 3.7 A). Catkin lengths of *S. arctica* were significantly different between years (Table 3.4), being shortest in 2001, 2005, 2006 and 2008 (Figure 3.7 B).

Significant differences between years in lengths of bulbil and flower sections of *P. viviparum* (Table 3.4) were driven by pronounced decreases and increases, respectively, in 2004 (Figure 3.7 C and D). This trend was present in both control and treated plots. Differences in bulbil section lengths between treatment types were most pronounced during the final three years of the study period and were smallest (insignificant) in 2004 and 2005 (Figure 3.7 C).

Although most target species showed significant interannual variation in reproductive characteristics, *Lupinus arcticus* was the only target species that showed a relationship with GDD (Figure 3.8). The number of *L. arcticus* inflorescences per basal rosette decreased with increasing GDD regardless of whether 2004 data were included. Peduncle lengths of *D. octopetala* and catkin lengths of *S. arctica* showed no clear trends with GDD. While reproductive measurements in 2004 did not seem atypical for *D. octopetala*, *L. arcticus*, or *S. arctica*, they were quite unusual for *P. viviparum* (Figure 3.8). Lengths of the bulbil and flower sections of *P. viviparum* were not responsive to GDD while it was between approximately 300 and 450; however in 2004 when GDD was 597, lengths were either much shorter or longer, than in more typical years. In 2004, the length of the flower section of the inflorescence was nearly five times greater than the 10-year mean, and the length of the bulbil section was 93% less than the 10-year mean. For each reproductive measurement of *P. viviparum* including data from 2004 changed the direction of the

trend (*i.e.* from negative to positive or vice versa) and made the relationship significant or nearly so (Figure 3.8 C and D).

Overall, few vegetative or reproductive indicators were responsive to annual variations in temperature. Correlations between target species measurements and other climate variables showed no clear indication of another abiotic factor dominating plant responses, although leaf length of *D. octopetala* and *S. arctica* were significantly related to total summer precipitation (Table 3.5).

3.3.2 Density of reproductive structures

Inflorescences of a total of 16 forb species, 8 graminoid species, and 4 shrub species were recorded in the annual counts. The species that were most abundant in terms of number of inflorescences were the evergreen shrub *D. octopetala* (38.2% of total inflorescences), deciduous shrubs *Salix reticulata* (15.8%) and *S. arctica* (8.7%), forbs *P. viviparum* (7.8%) and *L. arcticus* (6.3%), and the graminoid *Hierochloe alpina* (4.3%). Inflorescences of another graminoid *Festuca altaica,* were not particularly abundant (1.5%), but the species had one year of high flower production.

Only two species (*D. octopetala* and *P. viviparum*) showed significant responses to treatment (Table 3.6), with OTC plots yielding more inflorescences than controls in most years (Figure 3.9 A and C). Species within a growth form did not show the same pattern of annual variation. For example, while both forb species had fairly high interannual variation, *L. arcticus* inflorescences increased over time while *P. viviparum* inflorescences showed a decreasing trend over time (Figure 3.9 B and C). The significant effect of year on *F. altaica* inflorescences (Table 3.6) was driven by a large, sudden increase in flowering in 2005 (Figure 3.9 G). Only six of the

ten plots containing *F. altaica* flowered in 2005, but the remaining four plots had very low abundance of the species and did not produce flowers in any year.

Inflorescence counts that were standardised by average abundance were not related to GDD for any species. Absolute inflorescence counts of *L. arcticus* and *S. reticulata* were negatively related to GDD, and no other species had significant relationships (Figure 3.10; Table 3.7). The two *Salix* species had opposite responses to GDD. *Salix arctica* showed a positive trend with GDD that was significant only when 2004 data were excluded ($\rho = 0.728$; $P = 0.026$). Excluding 2004 data did not change any other relationships and so these analyses are not included here.

3.4 Allometry with annual measurements

Annual measurements of leaf lengths or widths all had highly significant positive relationships with leaf area and dry mass (Table 3.8). Bulbil section length of *P. viviparum* was the only reproductive indicator significantly related to a measure of reproductive output (Table 3.8). Increases in bulbil length yielded an increase in the number of bulbils, but were unrelated to average bulbil weight. Peduncle lengths of *D. octopetala* were unrelated to the total number of seeds and to the number of viable seeds produced. Catkin lengths of *S. arctica* were not directly related to the total number of seeds or to the number of viable seeds, but increases in catkin length were associated with a greater number of ovaries and ovary number was positively associated with the number of total and viable seeds (Table 3.8). Seed germination of *D. octopetala* was too low to assess relationships between annual measurements and seed germinability. No seeds of *P. viviparum* were found.

3.5 Community composition

A total of 40 vascular plant species were found in the study plots (Table 3.9) though average species richness per plot was less than half that value (Table 3.10). Of the three diversity indices calculated, only species richness changed significantly year to year and none of the measures differed between treatment types (Table 3.10).

There were differences in the overall community composition during the ten-year study period. Sørensen distances between plots in 1998 and 2008 were significantly different from zero for cover of vascular species ($t = 15.26$; df = 19; $P < 0.001$) and growth forms ($t = 10.28$; df = 19; $P < 0.001$). Unsurprisingly, mean distances (±SE) based on species data were greater than those based on growth forms (0.245 ± 0.016 and 0.157 ± 0.015, respectively). Change did not occur equally over the two five-year intervals, especially in terms of species composition, where distance values were significantly greater between 1998 and 2003 than between 2003 and 2008 (Table 3.11). There were no significant differences in distance values between control and experimental plots for either growth form abundance or species abundance. There was no significant interaction between interval and treatment type (Table 3.11), which suggests that composition changed equally in experimental plots as in controls.

The ordination confirmed that species composition was not distinctly different between treatment types (Figure 3.11). The final ordination required 60 iterations to reach a 2-dimensional solution. Stress was 13.66, suggesting that the graph was a reasonable representation of composition patterns in the data. Final instability was 10^{-5}. The ordination captured 90.5% of the variation in the data, with each axis expressing around 45%. All growth forms had correlation coefficients ≥ 0.35 with at least one ordination axis (Table 3.13). Graminoids, mosses, and deciduous shrubs were positively correlated with Axis 1, while lichens and *Dryas* were negatively correlated with Axis 1 (Figure 3.11; Table 3.12).

Though species composition changed from 1998 to 2008, changes were not uni-directional, nor were they uniform across plots (Figure 3.11). Some plots changed in one direction from 1998 to 2003 and then changed back along a similar direction, making composition in 2008 more similar to that in 1998 than in 2003, while others were most similar in 1998 and 2003 (Figure 3.11). There was no consistent direction of change from 1998 to 2003 or from 2003 to 2008 between plots (*e.g.* changes did not occur along the same axis). Results of the MRBP indicated that there were marginally significant differences in community composition between observers ($A = 0.012$; $P = 0.054$).

Table 3.1: Summary of results from a repeated measures ANOVA of average daily mean, minimum, and maximum temperatures during July of a warm (2004) and a cool (2008) summer at the Wolf Creek study site. The analyses were run with Day as the repeated factor and Treatment as a fixed factor. Statistics are based on the Huynh-Feldt adjustment to contend with lack of sphericity in the data. Significant results ($P \leq 0.05$) are in bold. Tests are based on 3 control and 2 OTC plots in 2004 and 3 control and 4 OTC plots in 2008.

Year	Temperature	Position	Variation	*F*	df	*P*-value
2004	Minimum	Air	Day	10.711	6.66, 19.95	**<0.001**
			Treatment	1.207	1, 3	0.352
			Day x Treatment	0.501	6.66, 19.95	0.815
		Soil	Day	17.830	3.13, 9.38	**<0.001**
			Treatment	0.130	1, 3	0.743
			Day x Treatment	0.417	3.13, 9.38	0.752
	Mean	Air	Day	33.597	15.10, 45.30	**<0.001**
			Treatment	0.056	1, 3	0.828
			Day x Treatment	0.985	15.10, 45.30	0.486
		Soil	Day	40.818	3.09, 9.28	**<0.001**
			Treatment	0.080	1, 3	0.796
			Day x Treatment	0.428	3.09, 9.28	0.743
	Maximum	Air	Day	20.724	19.26, 57.78	**<0.001**
			Treatment	0.108	1, 3	0.764
			Day x Treatment	1.205	19.26, 57.78	0.285
		Soil	Day	30.257	2.92, 8.75	**<0.001**
			Treatment	0.003	1, 3	0.958
			Day x Treatment	0.688	2.92, 8.75	0.579
2008	Minimum	Air	Day	7.464	4.23, 21.13	**0.001**
			Treatment	0.163	1, 5	0.703
			Day x Treatment	0.514	4.23, 21.13	0.735
		Soil	Day	14.897	1.49, 7.47	**0.003**
			Treatment	4.311	1, 5	0.093
			Day x Treatment	1.234	1.49, 7.47	0.328
	Mean	Air	Day	29.235	4.86, 24.28	**<0.001**
			Treatment	0.452	1, 5	0.531
			Day x Treatment	0.993	4.86, 24.28	0.441
		Soil	Day	17.772	1.60, 8.01	**0.002**
			Treatment	1.364	1, 5	0.295
			Day x Treatment	1.075	1.60, 8.01	0.369
	Maximum	Air	Day	23.409	4.70, 23.49	**<0.001**
			Treatment	3.062	1, 5	0.141
			Day x Treatment	1.386	4.70, 23.49	0.267
		Soil	Day	19.298	2.67, 7.94	**<0.001**
			Treatment	0.218	1, 5	0.660
			Day x Treatment	0.984	2.67, 7.94	0.422

Table 3.2: A summary of results from multiple regression analyses relating summed temperature deviations in OTCs relative to controls (ΔT; °C) to ambient temperature (T; °C), wind speed (W; m/s), and cloudiness (C; 0-5 ordinal classes with 0 being least cloudy and 5 being most). Temperature deviations are based on data from the study plots. Data for predictor variables are from the Whitehorse International Airport (Environment Canada 2009a), except ambient temperature which used measurements of above ground temperatures from the control plots at the study site. Regression equations given in the table are the best models found using the backward stepwise elimination of variables. 'Total' is the mean daily sum of ΔT, 'Midday' and 'Night' are the total ΔTs from 10:00 to 14:00, and 0:00 to 4:00, respectively. 2004 and 2008 had the highest and lowest mean July temperatures, respectively (Figure 3.1). 2003 had the greatest positive temperature deviations between experimental and control temperatures and 2006 had the least (Figure 3.4).

Year	**ΔT**	**Regression equation**[+]	**R^2**	**Model *P***
2003	Total	ΔT = 29.73** - 1.67W* - 5.16C**	0.382	**0.001**
	Midday	ΔT = - 0.92 + 0.53T*	0.194	**0.013**
	Night	ΔT = 2.67** - 0.23W[¥] - 0.58C*	0.228	**0.027**
2004	Total	ΔT = - 26.88[¥] + 2.97T*	0.164	**0.024**
	Midday	n.s.		
	Night	ΔT = - 6.67** + 0.472T*	0.178	**0.018**
2006	Total	ΔT = 6.07 - 9.85C**	0.405	**<0.001**
	Midday	ΔT = 5.94** - 2.67C**	0.335	**0.001**
	Night	ΔT = 8.94* - 0.81T* - 2.40C**	0.274	0.087
2008	Total	ΔT = 42.72** - 4.41T**	0.406	**0.001**
	Midday	ΔT = 9.38** - 1.20T**	0.331	**0.001**
	Night	ΔT = 0.19 - 0.90W[¥]	0.098	0.087

[+] Statistically significant at α = 0.1 ([¥]), 0.05 (*), or 0.01 (**); n.s. no variables were significant

Table 3.3: Summary of results of repeated measures MANOVAs on vegetative indicators of two target species indicating differences attributed to years (repeated factor) and OTC treatment (fixed factor). MANOVAs were performed where vegetative or reproductive variables of a species were correlated. Data are from the Wolf Creek study site from 2001 to 2008. Tests were carried out using ranked values. Significant results ($P \leq 0.05$) are in bold. Leaflet and petiole lengths were used in the MANOVA for *L. arcticus*. Variables used in the MANOVA for *S. arctica* can be found with the subsequent ANOVAs in Table 3.4.

Species	**Variation**	***F***	**df**	***P*-value**
L. arcticus	Year	2.702	14, 3	0.224
	Treatment	1.098	2, 15	0.359
	Year x Treatment	0.980	14, 3	0.587
S. arctica	Year	17.097	14, 4	**0.007**
	Treatment	1.822	2, 16	0.194
	Year x Treatment	1.035	14, 4	0.543

Table 3.4: Summary of results of repeated measures ANOVAs indicating differences in the vegetative (above double line) and reproductive (below double line) responses to the OTC treatment (fixed factor) and years (2001-2008; repeated factor) of four target species from the Wolf Creek site. Significant results ($P \leq 0.05$) are in bold.

Species	Measurement	Variation	*F*	df	*P*-value
D. octopetala	Leaf length	Year	2.974	7, 126	**0.006**
		Treatment	1.082	1, 18	0.312
		Year x Treatment	0.716	7, 126	0.659
P. viviparum	Leaf width	Year	3.489	7, 42	**0.005**
		Treatment	1.272	1, 6	0.303
		Year x Treatment	1.508	7, 42	0.191
	Number of leaves	Year	5.582	7, 42	**<0.001**
		Treatment	1.562	1, 6	0.258
		Year x Treatment	0.969	7, 42	0.466
S. arctica	Leaf length	Year	1.680	7, 119	0.120
		Treatment	3.553	1, 17	0.077
		Year x Treatment	1.178	7, 119	0.320
	Annual stem increment	Year	55.027	7, 119	**<0.001**
		Treatment	3.844	1, 17	0.067
		Year x Treatment	1.800	7, 119	0.093
D. octopetala	Peduncle length	Year	2.483	7, 126	**0.020**
		Treatment	6.124	1, 18	**0.024**
		Year x Treatment	2.154	7, 126	**0.043**
L. arcticus	Number of inflorescences	Year	1.370	7, 112	0.225
		Treatment	0.173	1, 16	0.683
		Year x Treatment	0.370	7, 112	0.552
P. viviparum	Length of bulbil section	Year	9.560	7, 42	**<0.001**
		Treatment	10.834	1, 6	**0.017**
		Year x Treatment	11.290	7, 42	0.279
	Length of flower section	Year	6.631	7, 42	**<0.001**
		Treatment	0.025	1, 6	0.879
		Year x Treatment	1.054	7, 42	0.409
S. arctica	Catkin length	Year	2.796	7, 98	**0.011**
		Treatment	0.623	1, 14	0.443
		Year x Treatment	1.285	7, 98	0.266

Table 3.5: Bivariate correlations (Pearson's r) between environmental variables from the current and previous years, and vegetative (above double line) and reproductive (below double line) measurements of target species. Plant data and GDD are from control plots at the study site. All other environmental data are from the Whitehorse International Airport (Environment Canada 2009b). Relationships significant at $P \leq 0.05$ and $0.10 \leq P \geq 0.05$ are in bold and italicised font, respectively. n = 10 in all cases.

			Current year				Previous year				
Species	**Measurement**	**Statistic**	**Snow fall**	**March Snow**	**Jan Temp**	**Summer Precip**	**Snow fall**	**March Snow**	**Jan Temp**	**Summer Precip**	**GDD**
D. octopetala	Leaf length	r	.152	-.222	-.100	-.062	.059	-.221	-.497	**-.640**	.070
		P	.674	.951	.783	.865	.870	.540	.144	**.046**	.848
L. arcticus	Leaflet length	r	.358	.152	.268	-.095	-.219	-.468	-.515	-.091	-.270
		P	.309	.674	.454	.794	.544	.172	.128	.803	.451
P. viviparum	Leaf width	r	.536	*.584*	.040	.128	.541	.386	.269	.293	-.341
		P	.111	*.076*	.913	.725	.106	.270	.453	.412	.335
S. arctica	Leaf length	r	*-.627*	-.114	-.115	.208	.541	.096	.404	.151	-.008
		P	*.052*	.755	.751	.563	.106	.792	.247	.678	.982
	Annual stem increment	r	.400	.167	-.120	-.341	-.329	.047	.075	.132	.262
		P	.253	.645	.741	.336	.353	.898	.836	.717	.464
D. octopetala	Peduncle length	r	-.392	-.226	.098	-.339	-.233	*-.618*	-.127	.362	-.300
		P	.262	.530	.788	.338	.518	*.057*	.726	.304	.399
L. arcticus	# of inflorescences	r	.146	-.146	.067	.134	-.030	.280	.287	.462	.164
		P	.688	.687	.854	.713	.934	.432	.422	.179	.651
P. viviparum	Bulbil section length	r	-.130	-.320	.396	.231	-.404	-.187	-.061	-.104	.135
		P	.721	.367	.257	.522	.247	.606	.867	.775	.711
	Flower section length	r	-.109	.010	-.539	-.287	.165	.296	.041	-.289	-.006
		P	.763	.978	.108	.421	.648	.407	.910	.418	.987
S. arctica	Catkin length	r	.017	-.073	-.208	**-.718**	.532	-.267	.054	-.524	-.047
		P	.963	.841	.564	**.019**	.113	.457	.883	.120	.898

Snowfall, total snowfall from October to March (cm); March Snow, depth of snow on the ground at the end of March (cm); Jan Temp, mean January temperature (°C); Summer Precip, total precipitation June to August (mm); GDD, growing degree days June to August.

Table 3.6: Summary of results of repeated measures ANOVAs on the number of inflorescences per unit average abundance of common vascular plant species from the Wolf Creek site. Results indicate differences associated with years (repeated factor) and OTC treatment (fixed factor). Data are from 2001 to 2008. Tests were carried out using ranked values. Significant results ($P \leq 0.05$) are in bold.

Species	Variation	*F*	df	*P*-value
L. arcticus	Year	8.955	7, 126	**<0.001**
	Treatment	0.470	1, 18	0.502
	Year x Treatment	0.517	7, 126	0.820
P. viviparum	Year	4.817	7, 63	**<0.001**
	Treatment	24.586	1, 9	**0.001**
	Year x Treatment	1.387	7, 63	0.226
D. octopetala	Year	4.928	7, 126	**<0.001**
	Treatment	4.660	1, 18	**0.045**
	Year x Treatment	1.741	7, 126	0.105
S. arctica	Year	1.589	1, 126	0.145
	Treatment	0.157	1, 18	0.697
	Year x Treatment	0.900	7, 126	0.509
S. reticulata	Year	2.070	7, 84	0.056
	Treatment	0.094	1, 12	0.764
	Year x Treatment	0.935	7, 84	0.484
H. alpina	Year	6.430	7, 77	**<0.001**
	Treatment	0.800	1, 11	0.390
	Year x Treatment	0.391	7, 77	0.905
F. altaica	Year	2.477	7, 42	**0.032**
	Treatment	0.566	1, 6	0.480
	Year x Treatment	0.869	7, 42	0.539

Table 3.7: Results of correlation analyses between the number of inflorescences of common species and growing degrees days (June 1 – August 31) from 1999 to 2008. Analyses were done using either absolute inflorescence counts or counts standardised by average abundance. Significant relationships ($P \leq 0.05$) are in bold.

	Absolute counts		**Standardised by abundance**	
	ρ	***P*-value**	**ρ**	***P*-value**
D. octopetala	-0.127	0.726	-0.273	0.446
L. arcticus	**-0.636**	**0.048**	-0.552	0.098
P. viviparum	-0.067	0.855	0.188	0.603
S. arctica	0.498	0.143	0.503	0.138
S. reticulata	**-0.842**	**0.002**	-0.333	0.347
H. alpina	0.280	0.434	0.382	0.276

Table 3.8: Summary of results of simple regression analyses of allometric relationships between leaf dimension (cm) and leaf area (cm^2) or dry mass (g) (above double line) and between lengths of reproductive structures (cm) and numbers or average dry mass (g) of reproductive units (seeds, bulbils, ovaries) (below double line). Data are from four target species from the Wolf Creek study site from July 2008. Relationships that are significant ($P \leq 0.05$) are in bold.

Species	x-variable	y-variable	r^2	n	*P*-value
D. octopetala	Leaf length	Leaf area	**0.804**	49	**<0.001**
	Leaf length	Dry mass	**0.712**	47	**<0.001**
L. arcticus	Leaflet length	Leaf area	**0.776**	44	**<0.001**
	Leaflet length	Dry mass	**0.653**	35	**<0.001**
P. viviparum	Leaf width	Leaf area	**0.682**	51	**<0.001**
	Leaf width	Dry mass	**0.414**	32	**<0.001**
S. arctica	Leaf length	Leaf area	**0.468**	51	**<0.001**
	Leaf length	Dry mass	**0.521**	40	**<0.001**
D. octopetala	Peduncle length	# of seeds	0.0001	35	0.941
	Peduncle length	# of viable seeds	0.0001	35	0.949
	Peduncle length	Germinability (%)	n/a	n/a	n/a
P. viviparum	Bulbil length	# of bulbils	**0.704**	34	**<0.001**
	Bulbil length	Average bulbil mass	0.001	33	0.851
S. arctica	Catkin length	# of total seeds	0.118	22	0.602
	Catkin length	# of viable seeds	0.047	22	0.350
	Catkin length	Germinability (%)	0.000	22	0.204
	Catkin length	# of swollen ovaries	0.154	25	0.053
	# swollen ovaries	# of total seeds	0.403	22	0.063
	# swollen ovaries	# viable of seeds	0.162	22	0.063

n/a insufficient data

Table 3.9: List of all vascular plant species found in the plots at the Wolf Creek study site between 1998 and 2008. Nomenclature follows the Integrated Taxonomic Information System (ITIS 2009). Several species have accepted subspecies or varieties that were not considered separately in this study.

Growth form	Family name	Species name	Taxonomic authority
Forbs	ASTERACEAE	*Antennaria alpina*	(L.) Gaertn
		Antennaria monocephala	DC.
		Arnica frigida	C.A. Mey ex Iljin
		Artemisia norvegica	Fries
		Saussaurea angustifolia	(Willd) DC.
		Tephroseris atropurpurea	(Ledeb.) Holub
		Tephroseris lindstoemii	(Ostenf.) A. & D. Löve
	BORAGINACEAE	*Myosotis alpestris alpestris*	F.W. Schmidt
	CAMPANULACEAE	*Campanula lasiocarpa*	Cham.
		Cerastium beeringianum	Cham. & Schlecht
	CARYOPHYLLACEAE	*Minuartia stricta*	(Sw.) Hiern.
		Silene acaulis	(L.) Jacq.
		Silene involucrate	(Cham. & Schlecht) Bocquet
		Stellaria longipes	Goldie
	CRASSULACEAE	*Rhodiola rosea*	L.
	EQUISETACEAE	*Equisetum* spp.	L.
	FABACEAE	*Lupinus arcticus*	S.Wats
		Oxytropis nigrescens	(Pallas) Fisch. ex DC.
	POLYGONACEAE	*Polygonum viviparum*	L.
	ROSACEAE	*Potentilla uniflora*	Ledeb.
	SAXIFRAGACEAE	*Saxifraga bronchialis*	L.
		Saxifraga reflexa	Hook.
		Saxifraga tricuspidata	Rottb.
	SCROPHULARIACAE	*Pedicularis capitata*	M.F. Adams
		Pedicularis lanata	Cham. & Schlecht
Graminoids	CYPERACEAE	*Carex microchaeta*	Holm.
		Carex ruperstris	All.
		Kobresia myosuroides	(Vill.) Fiori
	JUNACEAE	*Luzula confuse*	Lindeberg
		Luzula spicata	(L.) DC.
	POACEAE	*Festuca altaica*	Trin.
		Festuca brachyphylla	J.A. Schultes ex J.A. & J.H. Schultes
		Hierochloe alpina	(Sw. ex Willd.) Roemer & J.A. Schultes
		Poa arctica	R. Br.
		Poa alpina	L.
Shrubs	BETULACEAE	*Betula nana*	L.
	ERICACEAE	*Vaccinium uliginosum*	L.
	ROSACEAE	*Dryas octopetala*	L.
	SALICACEAE	*Salix arctica*	Pallas
		Salix reticulata	L.

Table 3.10: Measures of vascular plant diversity at the Wolf Creek study site in 1998, 2003, and 2008. Differences between treatment types and interactions between treatment type and year were not significant ($P > 0.10$). For a given diversity measure, values that do not share a letter were significantly different ($P \leq 0.05$). Values are means (± SE) from all study plots (n = 19 per year).

Diversity measure	Year	Average +/- SE
Species Richness	1998	12.4 ± 0.6^{a}
	2003	12.2 ± 0.6^{ab}
	2008	13.3 ± 0.6^{b}
Evenness	1998	0.68 ± 0.02^{a}
	2003	0.68 ± 0.02^{a}
	2008	0.68 ± 0.02^{a}
Shannon-Wiener Diversity	1998	1.70 ± 0.07^{a}
	2003	1.67 ± 0.07^{a}
	2008	1.75 ± 0.07^{a}

Table 3.11: Summary of results from repeated measures ANOVAs of Sørensen distances between plots for two five-year time intervals. Distance measures were based on relative abundance of growth forms or of vascular plant species found in the plots (see text for formula) at the Wolf Creek study site. Relationships that are significant ($P \leq 0.05$) are in bold. Mean distances (± SE) for each treatment type and interval combination are also presented (n = 10 for control; n = 9 for OTC).

	Interval	Treatment	Distance	Variation	*F*	df	*P*
Growth form	98-03	Control	0.142 ± 0.022	Interval	1.071	1, 17	0.315
		OTC	0.132 ± 0.024	Treatment	0.076	1, 17	0.768
	03-08	Control	0.143 ± 0.025	Interval x Treatment	0.973	1, 17	0.338
		OTC	0.169 ± 0.026				
Species	98-03	Control	0.279 ± 0.031	Interval	5.468	1, 17	**0.032**
		OTC	0.239 ± 0.033	Treatment	0.698	1, 17	0.415
	03-08	Control	0.225 ± 0.025	Interval x Treatment	0.259	1, 17	0.613
		OTC	0.204 ± 0.026				

Table 3.12: Kendall's correlation coefficients (τ) between each ordination axis and seven vegetative growth forms from an NMS ordination based on Sørensen distances. Coefficients represent the rank correlations between ordination scores and growth form variables. Stronger correlations ($\tau \geq 0.350$) are shown in bold font.

Growth form	τ	
	Axis 1	**Axis 2**
Forbs	0.212	**0.351**
Graminoids	**0.534**	-0.305
Deciduous shrubs	0.316	**-0.387**
Dryas	**-0.468**	**0.387**
Lichens	**-0.410**	0.236
Mosses	**0.375**	-0.331

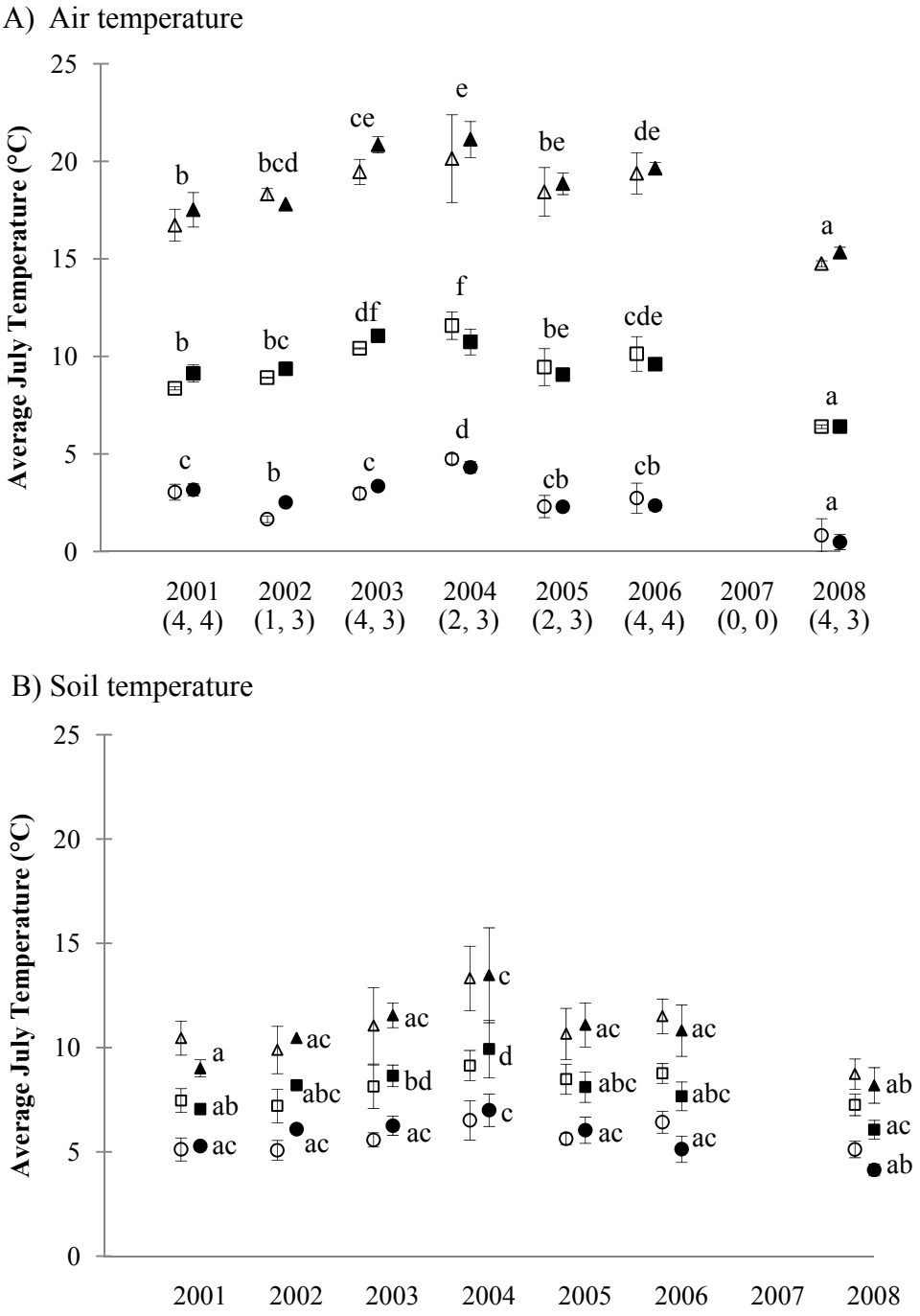

Figure 3.1: Average minimum (circles), mean (squares) and maximum (triangles) July temperatures for near-surface (A) air and (B) soil between non-manipulated controls (open symbols) and OTCs (filled symbols) at the Wolf Creek study site. Points represent means ± SE. Values are staggered along the x-axis to increase readability. For a given variable, values that share a letter indicate that years were not significantly different ($P \leq 0.05$). There were no significant differences associated with the OTC treatment. Sample size (control, OTC) is indicated below the years and is the same for air and soil temperatures. Data were missing for 2007.

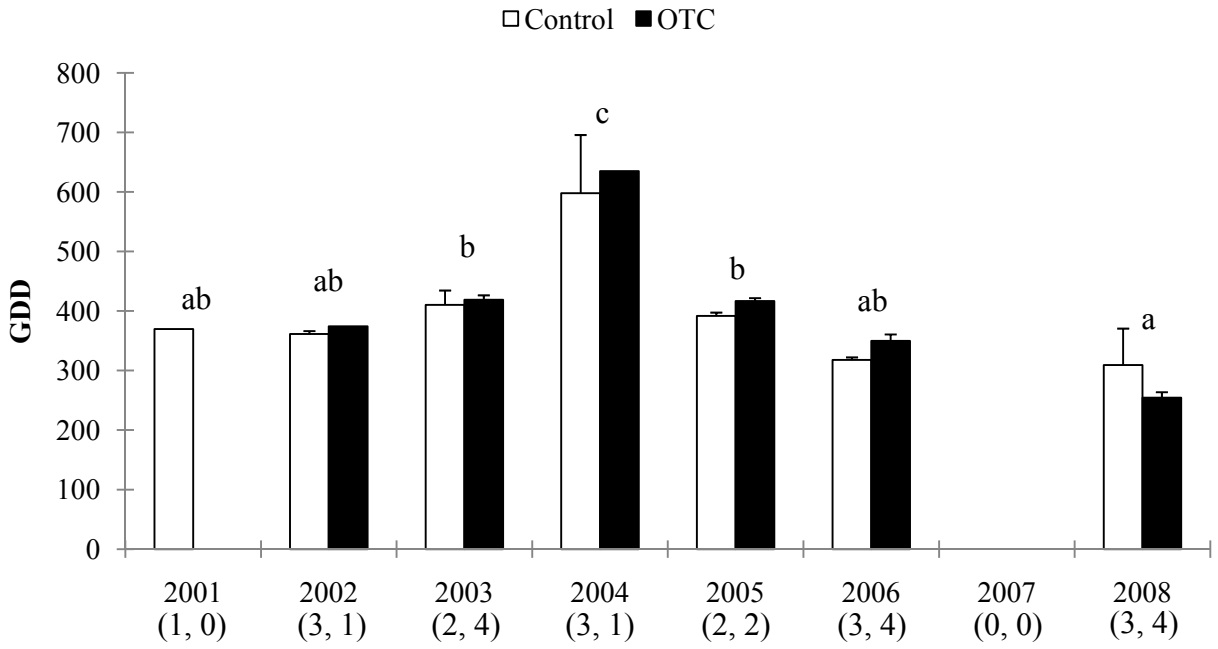

Figure 3.2: Total growing degree days (GDD) for June 1 to August 31 from 2001 to 2008 in control plots and OTCs. Values are means + SE. Sample size (control, OTC) is indicated below the years. Years that do not share a letter are significantly different ($P \leq 0.05$). There was no significant difference between treatment types. Data were missing for 2001 (OTC) and 2007 (both treatments).

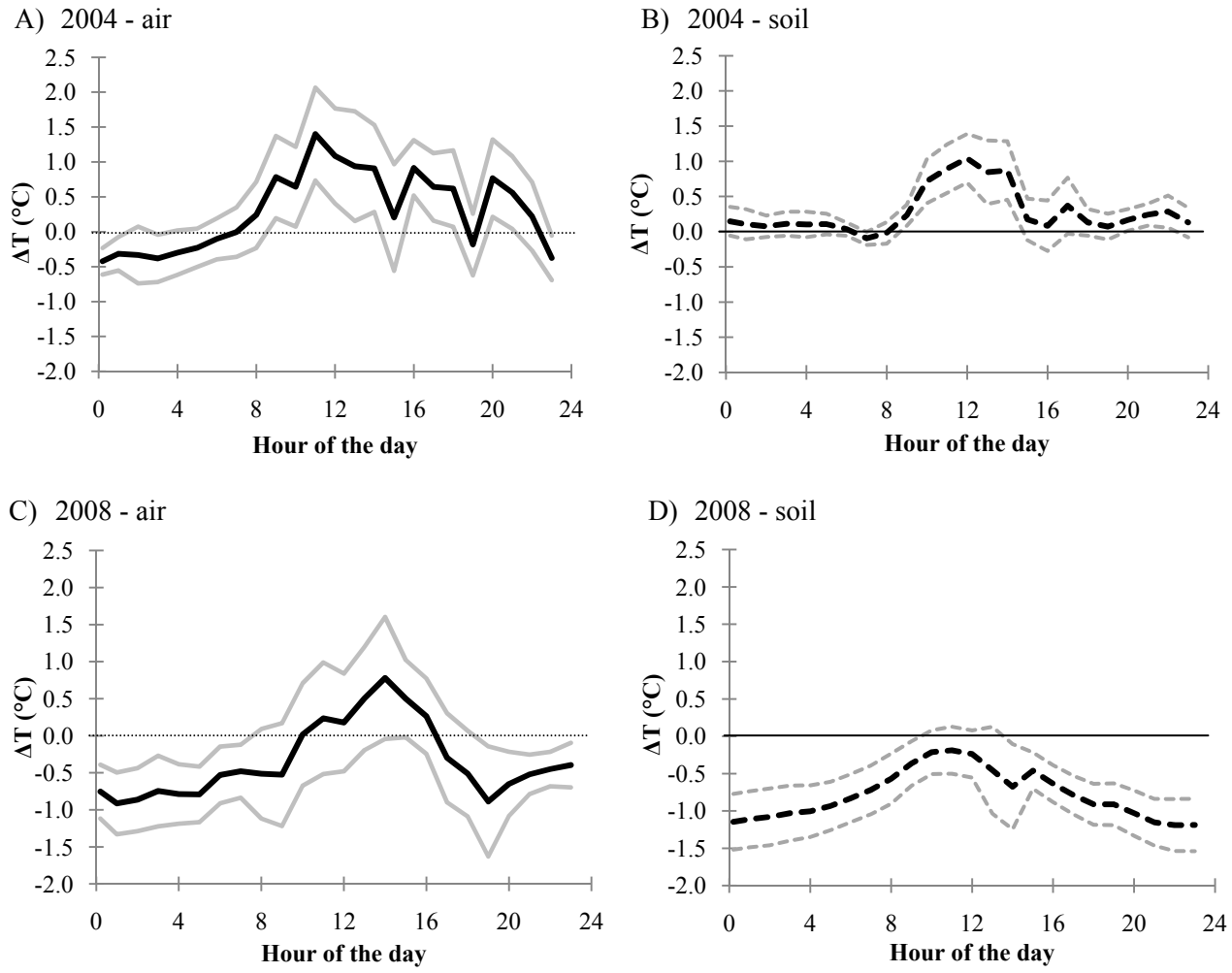

Figure 3.3: Diurnal patterns of air and soil temperature deviations (ΔT) between OTCs and control plots averaged for all days in July in a warm year (2004; A and B) and a cool year (2008; C and D) (n = 31). Deviations are control plot temperatures subtracted from OTC temperatures so that positive or negative values indicate that treated plots were warmer or cooler, respectively, than controls. Black lines represent means and grey lines indicate the 95% confidence interval around the means. Temperature deviations are different from zero if the entire confidence interval is above or below zero.

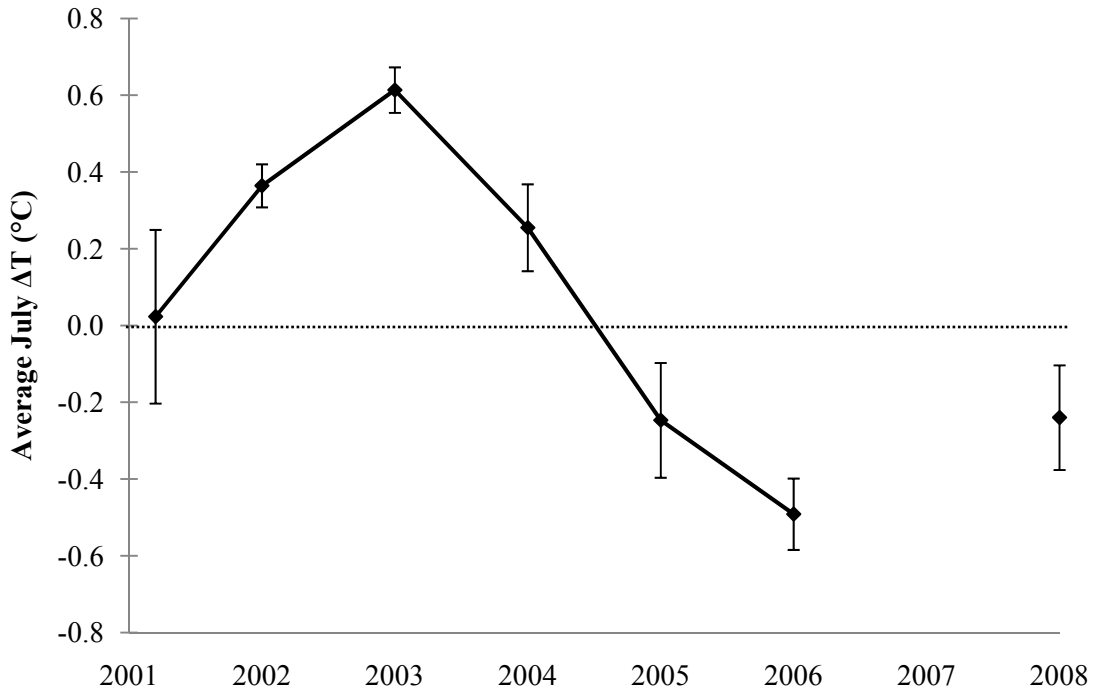

Figure 3.4: Average daily deviations in temperature (ΔT) between OTCs and control plots in July 2001 to 2008. Deviations are control plot temperatures subtracted from OTC temperatures so that positive or negative values indicate that treated plots were warmer or cooler, respectively, than controls. Data are from the Wolf Creek study site. Points are mean values ± SE (n = 28 in 2001, 31 for all other years). Data were missing for 2007.

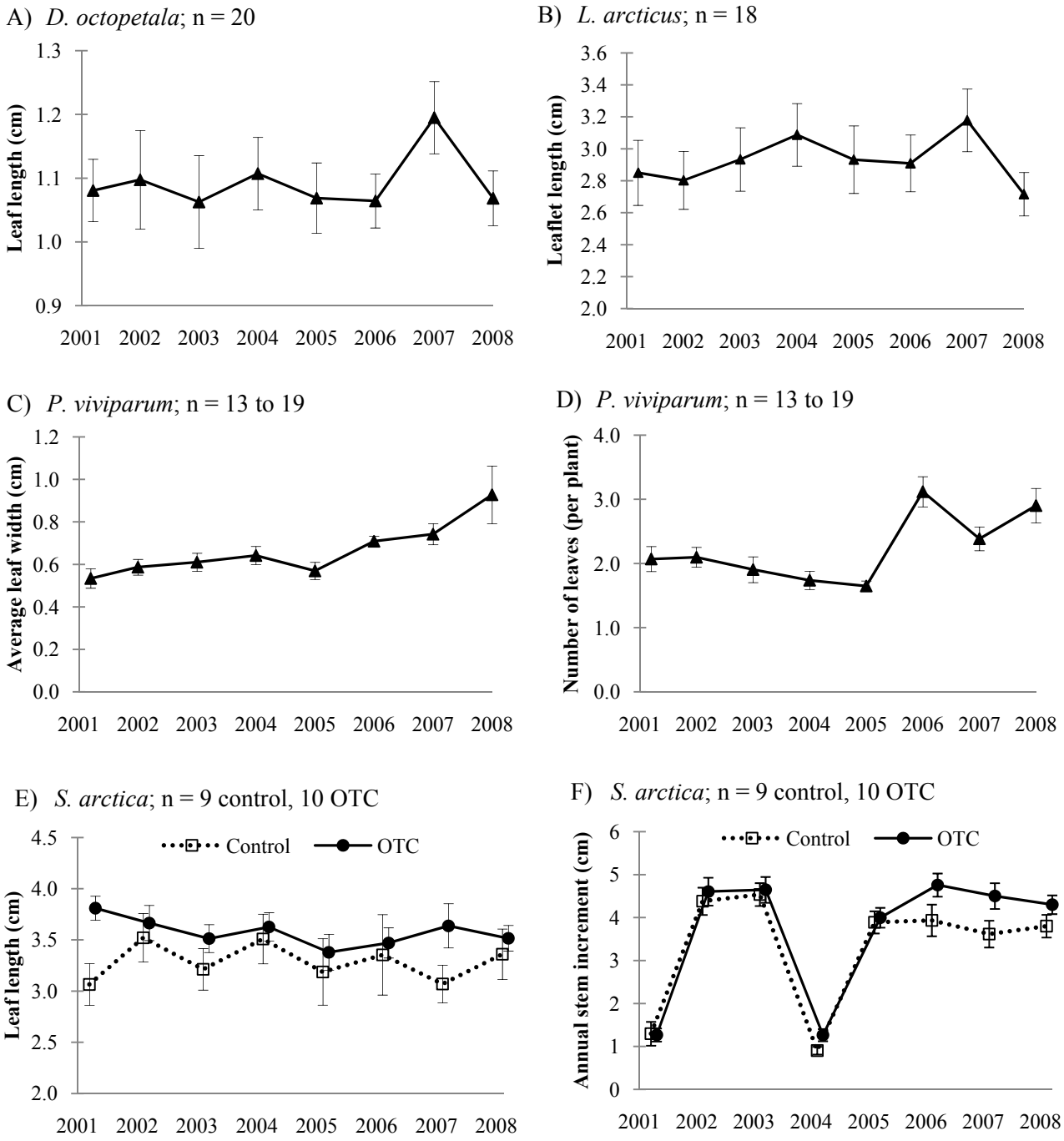

Figure 3.5: Annual variation in (A-E) leaf measurements and (F) current year stem lengths of target species from the Wolf Creek study site from 2001 to 2008. Data were pooled across treatment types except for *Salix arctica* where the effect of treatment was marginally significant (see Table 3.4). Points are mean values ±SE (sample sizes indicated in the panel caption) and have been staggered along the x-axis to increase readability.

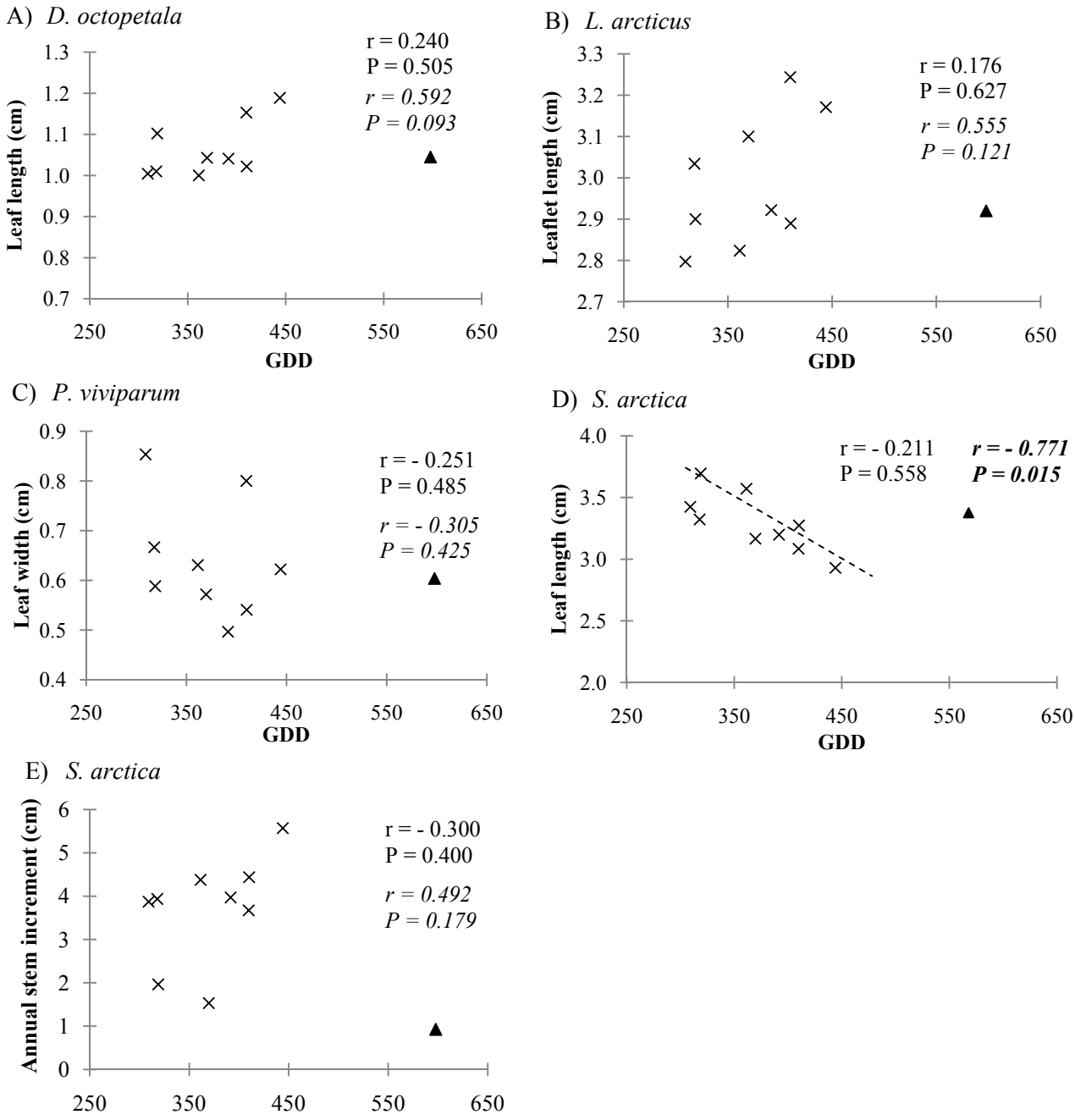

Figure 3.6: Relationships between measures of vegetative growth of the four target species and growing degree days (GDD; total from June 1 to August 31) from 1999 to 2008. Values for 2004 are denoted with a solid triangle as this summer was much hotter than is typical in southern Yukon. Correlation coefficients and *P*-values based on data that include (regular font) or exclude (italicised font) 2004 are shown (n = 10 or 9 years). A regression line is shown where the relationship is significant ($P \leq 0.05$) and the corresponding statistics are in bold font. GDD and plant values are means from control plots only (n plots = 1 to 4 for GDD; 10 for *D. octopetala* and *L. arcticus*, 6 to 8 for *P. viviparum*, and 9 to10 for *S. arctica*).

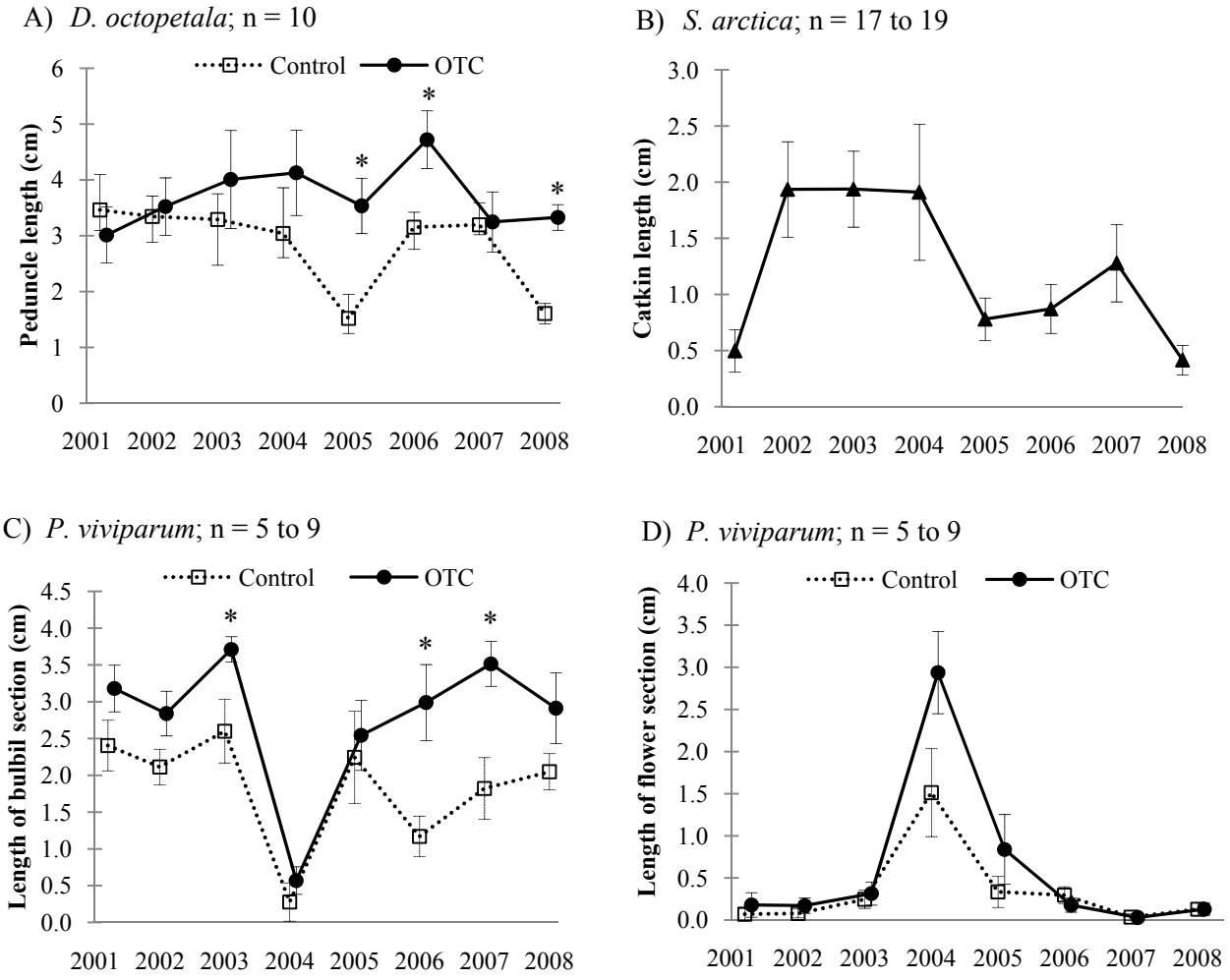

Figure 3.7: Lengths of reproductive structures of target species from 2001 to 2008. Catkin lengths of *S. arctica* were not different between treatments (Table 3.4) so data were pooled across treatment types. Years that were significantly different between treatment types for *D. octopetala* and *P. viviparum* are indicated (*). Points are mean values ±SE (sample sizes indicated in panel caption) and have been staggered along the x-axis to increase readability.

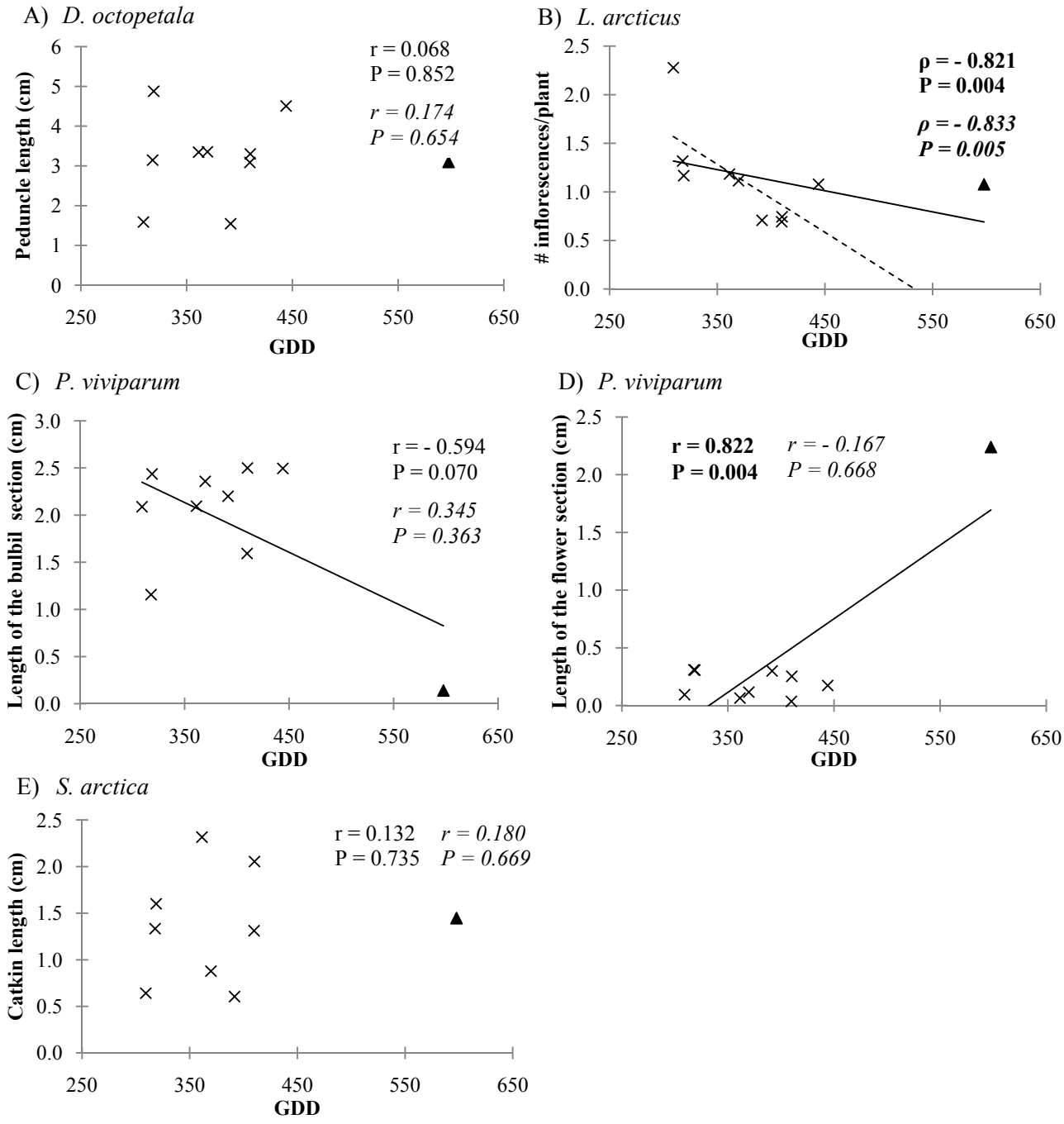

Figure 3.8: Relationships between reproductive measures of the four target species and growing degree days (GDD; total from June 1 to August 31) from 1999 to 2008. Values for 2004 are denoted with a solid triangle as this summer was much hotter than is typical in southern Yukon. Correlation coefficients and *P*-values based on data that include (regular font) or exclude (italicised font) 2004 are shown (n = 10, 9 except for *S. arctica* where n = 9, 8). A regression line is shown where the relationship is significant ($P \leq 0.05$) with (——) or without (- - -) 2004 data and the corresponding statistics are in bold font. GDD and plant values are means from control plots only (n = 1 to 4 for GDD; 10 for *D. octopetala* and *L. arcticus*, 5 to 7 for *P. viviparum*, and 7 or 9 for *S. arctica*).

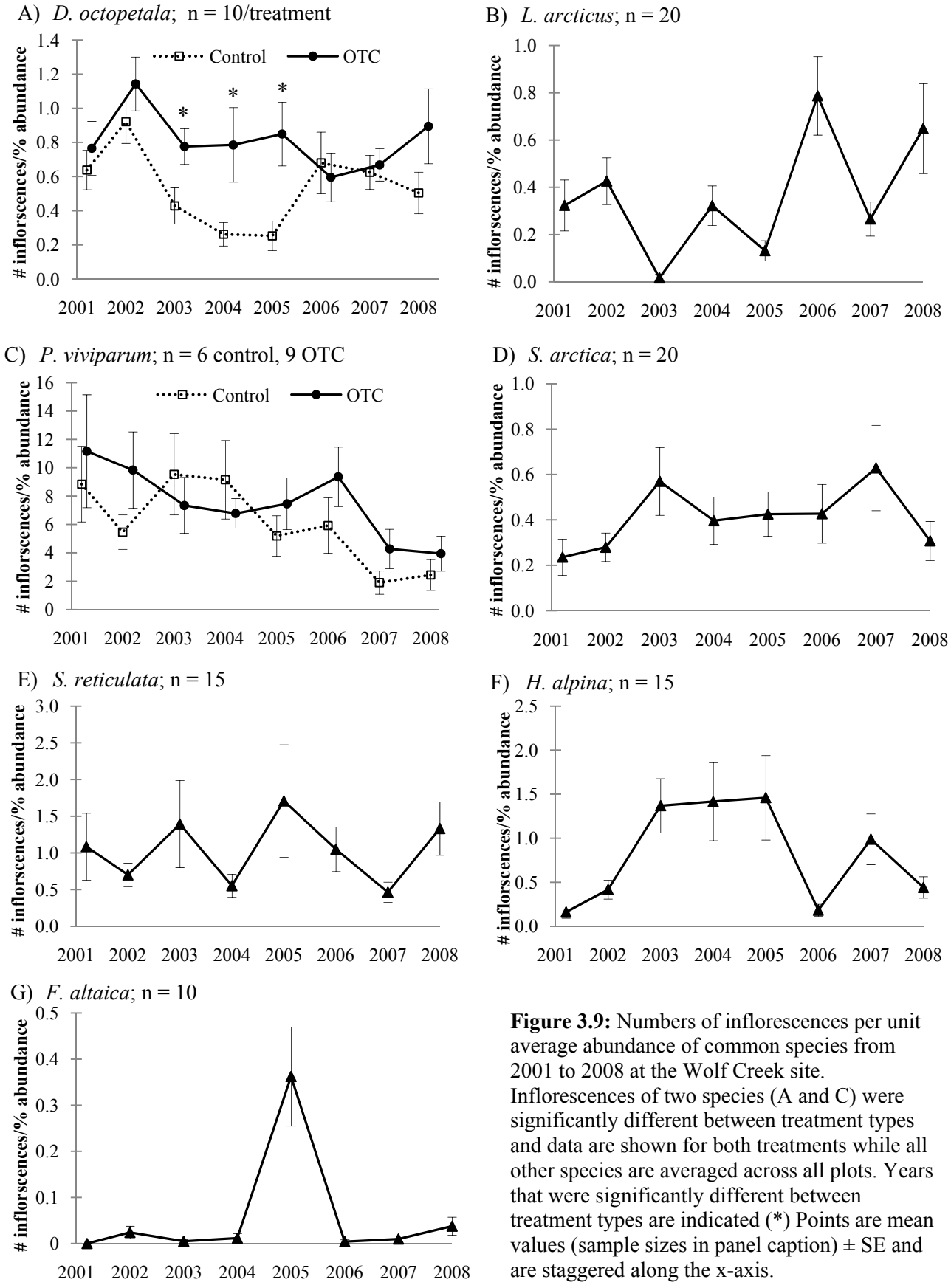

Figure 3.9: Numbers of inflorescences per unit average abundance of common species from 2001 to 2008 at the Wolf Creek site. Inflorescences of two species (A and C) were significantly different between treatment types and data are shown for both treatments while all other species are averaged across all plots. Years that were significantly different between treatment types are indicated (*) Points are mean values (sample sizes in panel caption) ± SE and are staggered along the x-axis.

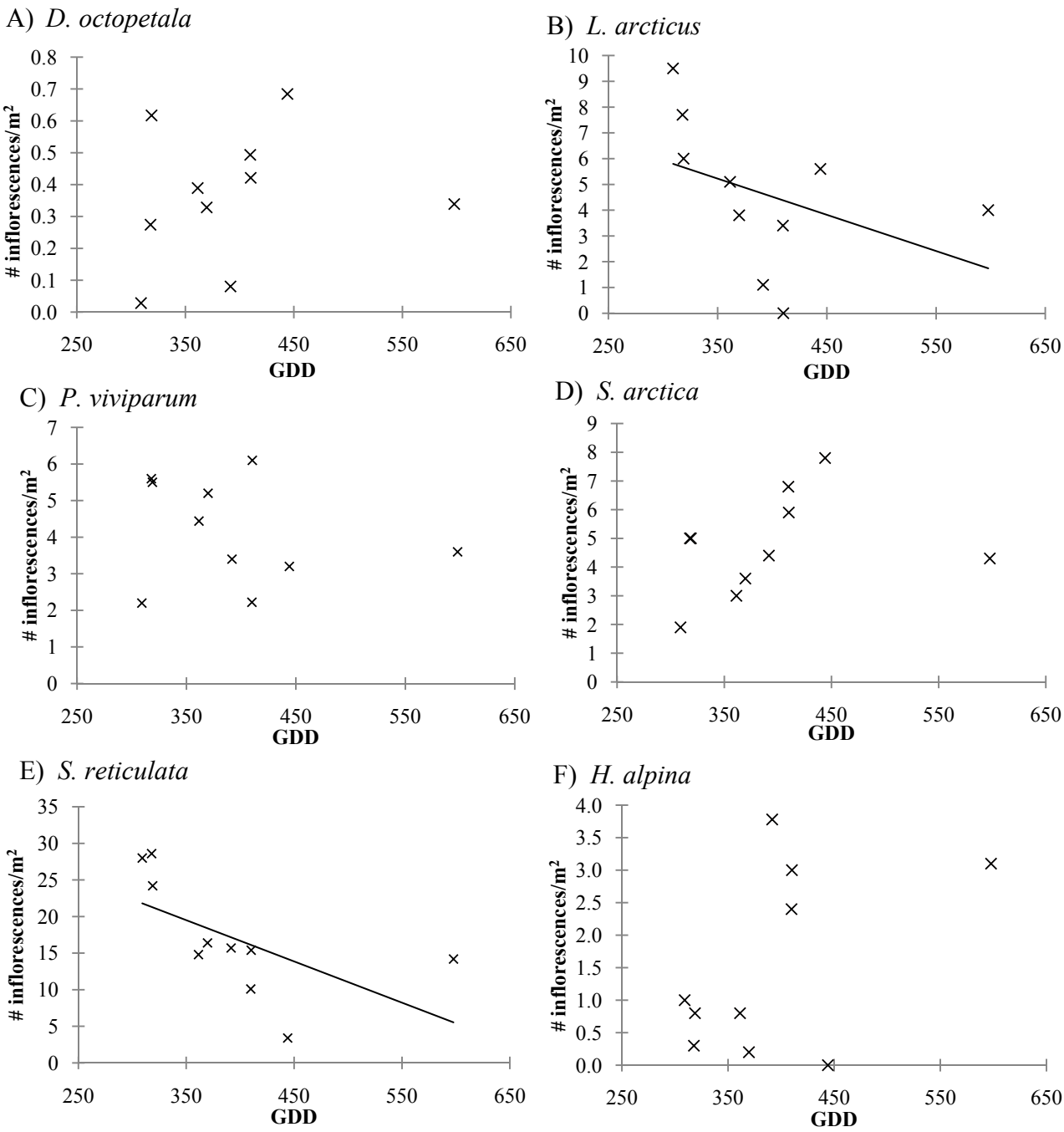

Figure 3.10: Relationships between the number of inflorescences of common species and growing degree days (GDD; total from June 1 to August 31) from 1999 to 2008. Correlation coefficients and *P*-values can be found in Table 3.7. A regression line is shown if the relationship is significant ($P \leq 0.05$). Plant variables and GDD are means from control plots only (n = 1 to 4 for GDD; n = 10 for each species).

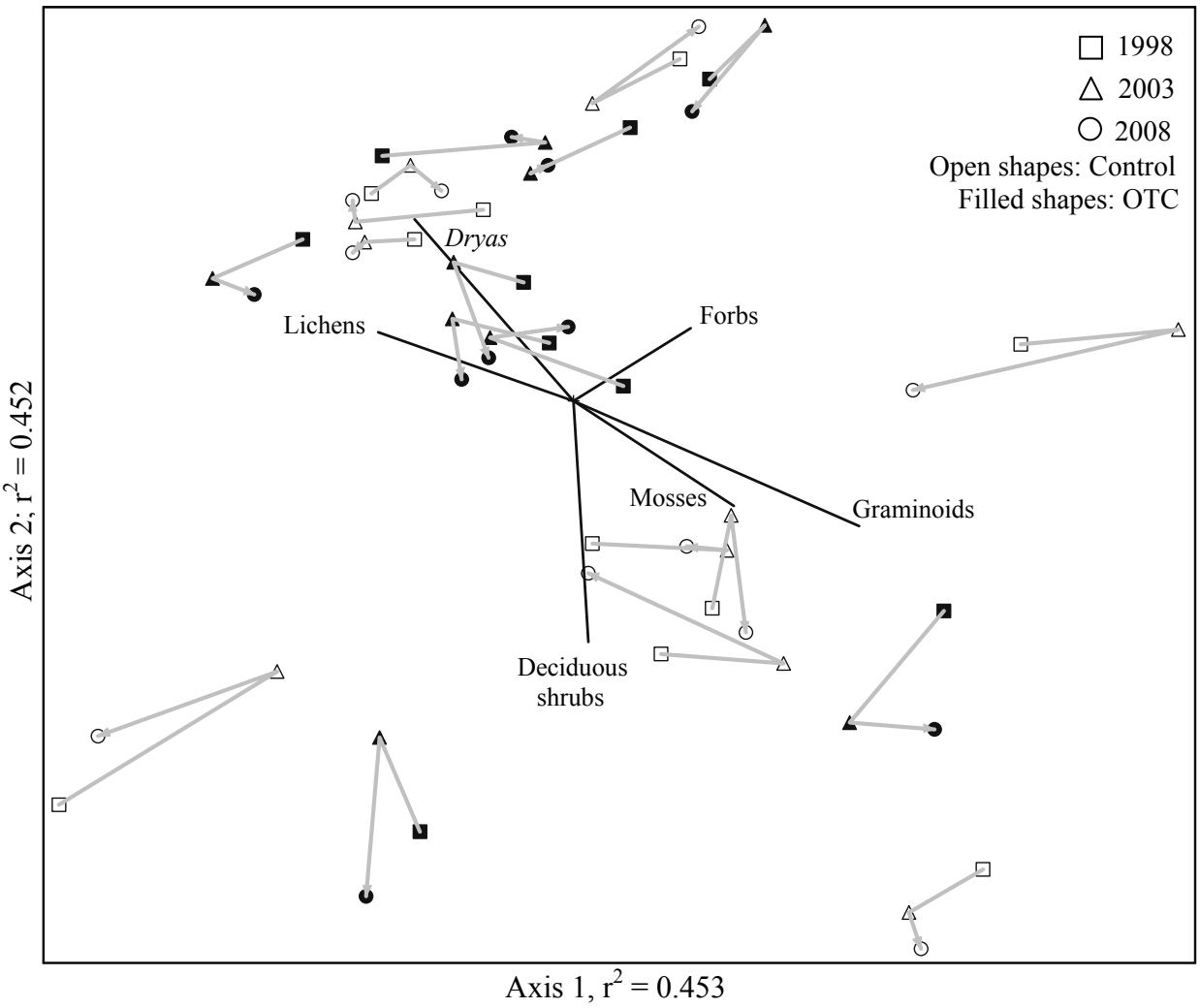

Figure 3.11: Non-metric multidimensional scaling (NMS) ordination of 19 study plots (10 control, 9 OTC) over three years (1998, 2003, 2008). The solution is 2-dimensional with a stress of 13.66. The r^2 value for an axis gives the proportion of variance expressed on that axis. Treatment type is indicated using open (control plots) or filled (OTCs) symbols. Symbols attached by grey lines represent the same plot measured in each of the three years with the arrow head pointing to 2008. A joint plot of growth forms has been overlaid where the length and angle of the black lines indicate the relative correlation ($\tau \geq 0.35$) of the growth form to the ordination axes (see Table 3.13 for exact values).

4.0 DISCUSSION

4.1 OTCs as an analogue for climate warming

There are several types of active and passive methods that can be used to increase temperatures in the field. Methods of active heating include burying electrical wires in the soil, laying fluid-filled pipes on the landscape, and using overhead heaters to increase surface and soil temperatures (reviewed in Shen and Harte 2000). These active methods usually afford the user more control over the degree of change than do passive techniques; however, active warming methods require some sort of power source and are therefore less feasible to implement at remote locations. Passive warming usually involves trapping solar radiation inside a structure to increase surface and soil temperatures. In the past this has been achieved by using tents with varying degrees of closure (e.g., Chapin and Shaver 1985b, Havström et al. 1993, Wookey et al. 1993, Parsons et al. 1994), but is now commonly accomplished using OTCs of various designs (e.g., Marion et al. 1997, Welker et al. 1997, Gugerli and Bauert 2001, Hollister et al. 2005a, b). Materials used in OTC construction have high transmittance in the visible wavelengths, but low transmittance in infrared waves (Marion 1996). The angled sides on the chamber increase its ability to trap heat. Since optimal transmittance occurs when radiation strikes the sides at 90°, the angled walls are also beneficial for transmitting solar radiation (Marion 1996).

OTCs have been preferred for passive warming because: 1) they are simple and inexpensive to construct and use, 2) they are structurally strong and can withstand high winds and extreme cold, 3) they can yield significant temperature enhancements, and 4) they minimise unwanted ecological effects (Marion 1996, Marion et al. 1997). The types and magnitude of unwanted effects depend on the specific design of the chamber, the characteristics of the site, and the research objectives. The only intended manipulation in this study was increased temperatures so

unwanted effects could have included increased frequency of temperature extremes, decreased wind speed, changes in gas concentration, decreased light transmission, changes to the water balance, and alterations to snow cover (Kennedy 1995, Shen and Harte 2000). All but the last listed effect are minimised by using chambers that have an open top rather than using fully enclosed tents (Marion et al. 1997). In this study, alterations to snow cover were avoided by putting up the OTCs only for the snow-free period each year. The chambers may also act as barriers to pollinators, dispersal agents, grazers, and pathogens (Shen and Harte 2000). Marion et al. (1997) suggested that truncated cone-shaped OTCs similar to those used in this study yield the least amount of shading, greatest light transmission, and least alteration to wind speeds and moisture regime than other open-topped warming techniques they tested (hexagonal OTCs, conical OTCs with higher walls, and rigid plastic corners).

By 2090 temperatures in the Arctic are projected to be approximately 3.7 ºC above the average from 1981 to 2000 (Kattsov et al. 2004). While OTCs do not always yield this magnitude of warming, they have been shown to be able to provide a significant temperature increase that represents a tradeoff between the magnitude of increase and unwanted experimental effects (Marion et al. 1997). The use of OTCs has been validated, at least from the plants perspective, when plant responses to experimental warming in a cool summer were very similar to those in control plots the following warm summer (Hollister and Webber 2000).

4.2 Temperature at Wolf Creek

In this study the application of OTCs did not have a significant effect on average monthly or daily July temperatures or GDD. Differences in temperature between treatment types were only apparent when hourly data were considered and the average degree of warming was never more than 1.5 °C. Both positive and negative effects of the OTCs were observed, and mean daily warming was often masked by night time cooling. The level of warming appeared to vary from year to year as temperature deviations were quite different between 2004 and 2008.

Previous studies have shown that OTCs can increase mean daily and monthly surface temperatures by 1 to 4 °C (e.g., Jones et al. 1997, Marion et al. 1997, Walker et al. 1999, Hollister and Webber 2000). While less common, night time cooling in OTCs, like that found in this study, has been reported previously (Gugerli and Bauert 2001, Stenström and Jónsdóttir 2006). The degree of warming achieved by OTCs is dependent on other climate variables such as solar radiation and wind speed (Marion et al. 1997). The low degree of warming found in this study is most likely due to the high winds at the site. Higher wind speeds promote the mixing of cool air from outside the OTC with the warmed air within, thereby decreasing the degree of warming. The magnitude of the effect of wind speed at the Wolf Creek site was likely underestimated in my regression analyses since wind data were from the Airport, which is less windy than the study site. It is likely that greater warming would have been achieved if OTCs had sat flush with the ground. It is also possible that the material used and/or condensation on the walls decreased the amount of solar radiation entering the OTCs (Kennedy 1995), although the effect of this would probably have been small.

The minimum projected increase in daily mean summer temperatures for the Arctic (under an approximate doubling of atmospheric CO_2 over levels in 2000 by 2100; IPCC Scenario A1B) is 1.2°C (Christensen et al. 2007). While no mean daily temperature increases were

achieved in this study, the midday warming that was attained is at the lower end of the projected range of temperature increase. Annual mean, minimum, and maximum temperatures have been increasing over the last century (Christensen et al. 2007), but minima have been increasing more than maxima both globally (Vose et al. 2005) and in high latitudes (Stafford et al. 2000, Tuomenvirta et al. 2000). This uneven increase in minimum and maximum temperatures has lead to a decrease in diurnal temperature range. In this study, temperature deviations were most positive at midday and most negative during the night, so that the daily range was greater in OTCs than in control plots. This is quite common in OTCs (e.g., Marion et al. 1997, Gugerli and Bauert 2001, Stenström and Jónsdóttir 2006) and appears to be a general limitation of the passive warming design.

Experimental plots experienced warming and cooling relative to controls, but the magnitude of each was small. It seems likely that only the most sensitive plant variables would be responsive to such small deviations. While temperatures were not very different between treatment types, there was substantial interannual variation in temperature recorded across the ten years of the study. Because of the lack of an effect of OTCs on temperature and high interannual variation, it is likely that many treatment responses may have been overshadowed by responses to natural variation in temperature.

Dunne et al. (2004) suggest that examining responses to experimental warming and natural temperature variation simultaneously may provide researchers with the most accurate way of assessing both long- and short-term responses to warming. Experimental temperature manipulations generate instantaneous changes usually on the short term (< ten years), yielding responses from only the most plastic variables. Examining effects of experimental warming in relation to natural temperature variation allows an understanding of the effects of temperature in the context of other factors (Hollister et al. 2005a). Theoretically, combining an experimental

warming treatment with natural temperature variation allowed me to better understand the influence of temperature on plants and predict future responses. Variables that responded to the treatment and to interannual variation are likely more responsive to temperature than those that were only responsive to one or the other. In this study however, experimental warming was so insubstantial that comparing plant responses between the treatment and natural variation may not be as informative. For the most part, responses to interannual variation will provide a general indication of how temperature influences plants at Wolf Creek, with results from the experimental treatment being of secondary importance.

4.3 Individual species responses to experimental treatment

There were few significant effects of observers on vegetative and reproductive plant traits. I think it likely that measurements may have yielded significant effects of observers due to chance. For example, it is reasonable that for a few traits one observer would measure more of the larger plant parts while another observer would measure more of the smaller ones. This could produce a statistically significant effect of observer, but would have little to do with the observers themselves. In addition, measurements of plant traits were fairly objective. Therefore, I conclude that the effects of observers on plant trait measurements were minimal.

Published studies of the effects of OTCs on vegetative characteristics show a wide variety of responses such that my results are consistent with some previous work, but not all. There were no significant vegetative responses to the experimental treatment for any of the target species at Wolf Creek. Vegetative responses of *D. octopetala* from previous studies are site specific. At sites from across the Arctic leaf characteristics of *D. octopetala* were larger in OTCs compared to controls in at least some years at all sites, but differences were only significant in the High Arctic (Welker et al. 1997). Other studies from the High Arctic have found both positive and negative

vegetative responses of *D. octopetala* to experimental warming (Welker et al. 1993, Wookey et al. 1995). Studies of *P. viviparum* at both high arctic and alpine sites found that vegetative measurements were not significantly different between OTCs and controls (Wookey et al. 1994, Gugerli and Bauert 2001), but significant effects of OTCs have been found (Molau 2001). In this study, leaves and annual stem increments of *S. arctica* tended to be longer in OTCs than in control plots, but differences were not significant. This is consistent with one study from the High Arctic that found leaves were generally longer and had greater mass in OTCs but that differences were not statistically significant (Jones et al. 1997).

Two species, *D. octopetala* and *P. viviparum,* had reproductive characteristics that were significantly different between treatment types. A larger response in reproductive compared to vegetative characteristics has been found in response to increased temperatures for both species previously (Wookey et al. 1994, 1995, Welker et al. 1997, Gugerli and Bauert 2001). Studies of reproductive responses of *S. arctica* to experimental warming have yielded mixed results. Jones et al. (1999) found longer catkins in OTCs compared to controls, but differences were not consistent between years, sites, or sex. In arctic Alaska, Jones et al. (1997) found vegetative measurements of *S. rotundifolia* to be significantly greater in OTCs but reproductive measurements were not different. Most published studies of *S. arctica* have been conducted in the High Arctic (Jones et al. 1997, 1999) where plants may be more temperature limited and responses to experimental warming are often larger (Wookey et al. 1993, Graglia et al. 1997, 2001, Welker et al. 1997). To my knowledge, *L. arcticus* has not been studied in the context of growth and reproductive responses to temperature. One study that compared ground cover from 1986 to that in 1999 at a site in northern Yukon indicated that cover of *L. arcticus* had increased markedly, potentially in response to warmer, drier conditions during this time period (Kennedy et al. 2001), but the effect of temperature was not assessed directly. Responses of other perennial

forbs to experimental warming indicate increases in both vegetative and reproductive measurements in OTCs versus controls (Molau 1997, 2001, Kudernatsch et al. 2008), but non-significant effects of OTCs have also been reported (Hollister et al. 2005a).

Differences between my results and those of other studies could be caused by two main factors. First of all, experimental warming at the Wolf Creek site was much less than has been reported in other ITEX studies (Marion et al. 1997, Hollister and Webber 2000). Plants at Wolf Creek may be more sensitive to temperature than was found using OTCs, but the degree of warming achieved in this study may have been insufficient to generate a measurable response. Secondly, plants in milder sites such as Wolf Creek are often less temperature limited than those in the High Arctic such that small increases in temperature may yield comparatively small or non-significant responses.

4.4 Individual species responses to interannual temperature variation

Using GDD as an indicator of temperature response was appropriate in this study since GDD defines the growing season for plants (Maxwell 1992) and captures temperature conditions throughout the growing season. Measures of heat accumulation are often used as an indicator of temperature effects (Molau 2001, Hollister et al. 2005a, b). Molau (1996b) stated that GDD shows a better correlation with plant growth than does thawing degree days (TDD). Thawing degree days have been used instead of GDD at colder sites where growth begins near 0 °C (Hollister 1998). In this study, regression results were not different when plant response variables were compared to GDD, mean June temperature, or mean July temperature (data not shown).

Unlike with the experimental treatment, there were a number of plant response variables that were significantly different between years. However, species did not respond similarly to annual variations in temperature. Leaf length of *S. arctica* was the only vegetative characteristic that was

related to GDD. Leaf lengths of *D. octopetala* showed trends of increase with increasing GDD, but values associated with the high GDD of 2004 were comparatively low. This could suggest that temperatures in 2004 were too warm for optimal leaf growth of this species. Species were also individualistic in terms of their reproductive responses to different years. Reproductive structures of *D. octopetala* and *S. arctica* were unrelated to GDD while the numbers of inflorescences of *L. arcticus* and *Salix reticulata* were negatively related. Negative responses to GDD may be results of changing competitive balances between species where one species is competitively repressed by another that responds positively to increased temperatures (e.g., Dormann et al. 2004). Negative responses in individual traits may also be because of changes in resource allocation within the plant, where for example, vegetative growth is more heavily favoured by warming than is reproductive investment (e.g., Jónsdottir et al. 2005a).

In some cases different response variables on the same plant showed dissimilar responses to temperature. While leaf length of *S. arctica* was negatively related to GDD, annual stem increment was unrelated. This indicates that different aspects of growth within a species may respond differently to the same climate conditions. Plants are responsive to other environmental variables besides temperature (Walker et al. 1994, Molau 1997). Therefore, temperature may be an important determinant of leaf length of *S. arctica*, while other variables are more important for annual stem increment.

The largest response to conditions in 2004 was seen in the reproduction of *P. viviparum.* Bulbil and flower section lengths of *P. viviparum* were not related to GDD under typical variation, but the high value of GDD in 2004 was associated with large decreases in bulbil section length and large increases in flower section length. The ratio of flowers to bulbils is at least partially under environmental control (Bauert 1993). The lack of response of bulbil and flower sections to typical variation in GDD, combined with large responses to high GDD

suggests that bulbil and flower section lengths of *P. viviparum* have non-linear responses to temperature.

I have shown that the length of the bulbil section of *P. viviparum* is positively related to the number of bulbils produced on an inflorescence. Not enough inflorescences bearing flowers were found to test for a similar relationship with flowers, but it seems logical that one would exist. The number of bulbils has been shown to be negatively related to the number of flowers (Bauert 1993, Fan and Yang 2009) such that there is a tradeoff between sexual and asexual reproduction (Law et al. 1983). In 2004 there were significant increases in the lengths of flower sections while the total length of the inflorescence was unaltered (data not shown). This indicates that the total reproductive investment was approximately the same, but that the mechanism changed from primarily bulbils to primarily flowers. A greater number of flowers under warmer conditions does not necessarily indicate a greater number of seeds. Successful seed set in *P. viviparum* is very rare because of low seed production and the abortion of young sporophytes (Diggle et al. 2002). Increases in flower production at the detriment of bulbil production may therefore lead to overall decreases in reproductive output. Whether or not seed production may be improved under increased temperatures is unknown, but if not, climate warming may lead to a considerable decrease in reproduction of this species.

The considerable increase in the number of inflorescences of *Festuca altaica* in 2005 may be a lag response to conditions in 2004. Floral preformation is common in arctic and alpine species (Bliss 1962, Billings and Mooney 1968) and has been found in a sub-Antarctic species of *Festuca* (Walton 1982). Despite floral preformation being so common, *F. altaica* was the only species to show a potential lag response to the warm conditions of 2004. Molau (2001) reported that the number of *D. octopetala* flowers reflects the previous year's climate, but this was not found in the present study.

My results may suggest that reproductive buds of *P. viviparum* are able to switch from bulbil to flower early in the current growing season under very warm conditions. It has been shown that the numbers of bulbils and flowers to be borne on an inflorescence are determined the year before maturation (Diggle 1997). A lag response was not evident in 2005 for *P. viviparum* and the response to the warm temperatures in 2004 may have been observed in that year. The nature of the relationship between bulbil production and flower production has been shown to vary across sites and under different biotic and abiotic conditions (Law et al. 1983, Bauert 1993, Totland and Nyléhn 1998, Fan and Yang 2009) so that this ability to switch reproductive buds in the year of emergence may vary among populations.

The number of inflorescences of a species was significantly related to GDD when absolute numbers were considered, and not when counts were standardised by average abundance. The absolute number of inflorescences was significantly related to abundance for a number of species (*D. octopetala, L. arcticus, S. reticulata*, and *H. alpina*; data not shown) so that relationships or trends between absolute numbers of inflorescences and GDD may actually be a product of changes in species cover with GDD. I was unable to measure this relationship directly because abundance was only measured in three years.

4.5 Comparisons of species responses to experimental treatment and interannual temperature variation

Species varied in the degree to which responses were consistent between experimental treatment and interannual variation. Leaf length of *S. arctica* was negatively related to GDD, but there was a trend towards longer leaves in OTCs than in controls. Since experimental warming was so low and the negative relationship with GDD quite strong, it seems likely that leaves responded to another factor being manipulated by the chambers. Wind speed may have been

decreased in OTCs compared to control plots (Kennedy 1995, Marion et al. 1997), though it was not measured in this study. Marion et al. (1997) suggested that protection from the wind may play a larger role than increased temperature in providing an improved environment for plants within OTCs. This may be especially important at a windy site like Wolf Creek. Slightly longer annual stem increments in *S. arctica* were perhaps also the product of plants having been sheltered from wind. Differences between treatment types did not appear until the later years of the study which may be indicative of a lag response to the more favourable environment. All other vegetative measurements had insignificant differences between treatment types and no relationships with GDD, and can therefore be considered unresponsive to temperature at least within the range of GDD observed in this study.

Dryas octopetala and *P. viviparum* exhibited increases in both the size and number of reproductive structures in OTCs relative to controls. However none of these response variables were significantly related to GDD in typical years. Bulbil and flower section lengths of *P. viviparum* that were markedly different in 2004 compared to other years suggests that these characteristics are responsive to high temperatures, but not to those that are currently more typical. Bulbil sections were shorter in 2004 which was the opposite of the response to the experimental treatment where bulbil sections were longer in OTCs compared to controls. Plants of both *D. octopetala* and *P. viviparum* in OTCs were likely responding to another aspect of the environment what was being modified by the chambers.

4.6 Interpretations of observed plant responses

Measurements of target species were made annually on the same plant which required that measurements be non-destructive. However, these measures are irrelevant to the plant unless they are related to some aspect of plant survival, growth, or reproduction. Since annual leaf measurements were highly significantly related to leaf area and leaf mass, it can be assumed that the annual measurements were reasonable indicators of processes that are important from the plant's perspective. Leaf area can be used to describe light capture by the plant, and in expressing tradeoffs through surfaces such as that between carbon gain and water loss (Farquar et al. 2002, Wright et al. 2004), while mass is more often related to photosynthetic capacity, dark respiration rate, and leaf nutrient levels (Wright et al. 2004). Interannual variation in temperature likely affected leaf area and mass of *S. arctica* via changes in leaf length, but leaf area and mass of other target species were unaffected. The absence of any significant vegetative responses suggests that the OTCs did not affect leaf area or mass in the target species.

Not all reproductive indicators measured in this study were related to the more biologically meaningful variables considered. It had been found previously that longer peduncles of *D. octopetala* produced a greater number of seeds (Welker et al. 1997). In this study peduncle lengths were not related to total number of seeds or the number of viable seeds. Consequently, longer peduncles in OTCs at this site cannot necessarily be interpreted as indicating an increase in seed number. However, since *D. octopetala* is a wind dispersed species (Welker et al. 1997), longer peduncles may increase dispersal distance (Savile 1972). Unlike *D. octopetala*, longer reproductive structures of *P. viviparum* were related to increased reproductive output. Length of the bulbil section of *P. viviparum* was positively related to the number of bulbils produced. This result is similar to that of Gugerli and Bauert (2001) who found that the number of bulbils was significantly correlated with the length of the whole inflorescence stalk (they did not measure

length of the bulbil section). At Wolf Creek, longer bulbil sections in OTCs may indicate increases in bulbil production. Longer catkins of *S. arctica* were associated with a greater number of swollen ovaries, but not with a greater number of viable seeds. However, more swollen ovaries yielded more viable seeds suggesting that the number of viable seeds is affected by multiple factors.

Target species used in this study were chosen to represent various growth forms. However, results of this study do not indicate that species within a growth form show similar responses to temperature which is consistent with previous studies (Chapin et al. 1995, Chapin and Shaver 1996, Dormann and Woodin 2002). My results can therefore not necessarily be scaled up to indicate general responses for whole growth forms. Chapin et al. (1996) help provide further support for this. They grouped 37 species into growth forms using cluster analysis based on numerous traits expected to influence plant responses to climate, responses to disturbance, resource acquisition, and nutrient use and competitive balance. Their study only involved one of the target species examined at Wolf Creek, but congenerics of the other three species were examined. *Salix* species and *Polygonum bistorta* were grouped into deciduous shrubs and forbs, respectively. *Dryas integrifolia* was classified as an evergreen shrub, but as quite distinct from other species in the same growth form. *Lupinus arcticus* was classified as being quite different from species in any other group such that the authors suggested it might be a keystone species with a unique ecological role. Based on the classification of Chapin et al. (1996), responses to temperature of *S. arctica* and *P. viviparum* in the present study are potentially representative of deciduous shrubs and forbs, respectively. Responses of *L. arcticus* and *D. octopetala* should be taken as that and not as general growth form responses. Regardless of growth form congruity however, responses to temperature of all four target species are important to the future functioning of this ecosystem.

4.7 Community composition

Community composition was not different between treatment types. This in contrast to several previous studies that have generally found decreases in species richness, increases in shrubs and graminoids, and decreases in lichens and bryophytes in response to experimental warming (Cornelissen et al. 2001, Hollister et al. 2005b, Wahren et al. 2005, Walker et al. 2006). Insignificant differences in community composition between treatment types in this study were likely a result of insufficient warming to generate a response from individual plants as mentioned in the preceding sections.

Community composition did change over time, but the changes were not uni-directional. This is unsurprising with only three years of data since communities routinely change year to year in response to interannual variation (Shaver et al. 2001). Ambient temperature did not change in a certain direction over the ten years that the study took place so it is perhaps unsurprising that communities did not either. Epstein et al. (2004) simulated an increase in temperature of 3 °C over 50 years for low arctic Alaska and found that changes in community composition that are driven by climate forcing, as opposed to natural variation, will likely not be observable for 15 or 20 years after initial sampling. They further predicted that some changes would take even longer to detect. The changes that were observed during the present study were due to natural variation in several environmental conditions, and directional changes in community composition will likely only be noticeable on a multi-decadal time scale against this background of annual variation.

While the point-frame method for assessing species cover is less subjective than other methods (Goodall 1952, Bonham 1989), there are certain caveats to consider. Several different researchers collected point-frame data over the duration of the study. This could have lead to different interpretations of the ground cover. The effect of this in 2008 was marginally

significant. It is likely that observer bias was present between years also and is responsible for some of the variation in composition between sampling times. It seems intuitive that the thickness of the pin used would have an impact on which species are hit and how many hits are recorded. Wilson (1963) reported that a doubling of pin diameter doubles the error in estimates of what he calls "relative frequency." However, both Wilson (1963) and Goodall (1952) report that the effect of pin size is much less substantial when relative abundance is considered in the analyses. Another factor to consider with this method is the effect of growth form on the number of hits recorded. Shaver et al. (2001) found that the number of hits on vegetation per pin drop was higher for species with broad, horizontally oriented leaves, whereas, for example, graminoids registered far fewer. Since this study was concerned with changes over time and the same methodology was used each year, errors from these two factors were minimised and the method should still provide a good indication of change over time.

4.8 Conclusions

Results of this study are consistent with a large body of literature that suggests that plants in arctic and alpine ecosystems respond individualistically to temperature (Chapin and Shaver 1985b, Chapin and Shaver 1996, Molau 1997, 2001, Kudo and Suzuki 2003). Species within a growth form did not have similar vegetative or reproductive responses to temperature at Wolf Creek. Responses of target species also differed from those observed at other sites, which makes generalising about plant responses to temperature across the Arctic very difficult, and perhaps even inadvisable (Van Wijk et al. 2004). I also found that different characteristics of a single species can have different responses to temperature, as evidenced by the contrasting vegetative responses of *S. arctica.* Responses to temperature that are species-, site-, and trait-specific restrict

our ability to reliably predict future impacts of climate warming on tundra plants and plant communities.

For the most part plants measured at Wolf Creek were not very responsive to observed variations in temperature. This seems surprising in an environment where plants are living below their temperature optima (Tieszen et al. 1981) and suggests that other factors are important in controlling plant responses. The experimental treatment was not a strong test of whether or not plants are responsive to temperature since temperature differences between OTCs and controls were minimal. However, a few plant variables were larger in OTCs which suggests that plants responded to another factor being manipulated by the chamber. Since responses were small, it is likely that the manipulated factor(s) had a relatively minor effect on the plants. The study of annual responses to temperature revealed only four measurements that were responsive to interannual temperature variation within typical range. A large increase in temperature such as that seen in 2004 did yield substantial responses from variables that were otherwise unresponsive, but this was only evident in three traits. It is most likely that temperature is not a strong limiting factor for plants at Wolf Creek, but that temperature may act indirectly via its influence on other factors, the most probable being nutrient availability. Warmer temperatures have been shown to increase the amount of nutrients available to plants (Hobbie 1996, Nadelhoffer et al. 1997), and nutrients are often also limiting in arctic and alpine habitats (Chapin 1987). Studies that manipulated both temperature and nutrients have commonly found stronger responses to nutrient addition than to experimental warming (Chapin and Shaver 1985b, Wookey et al. 1993, Graglia et al. 1997, Dormann and Woodin 2002, Van Wijk et al. 2004). Though nutrients were not measured in this study, results from other tundra studies suggest that variations in temperatures in the Wolf Creek area may yield indirect responses to temperature via their influence on nutrient availability.

Decadal changes in plant community composition at this site can be expected to be small and slow as individualistic species responses buffer large community level changes. A high degree of warming such as that seen in 2004 may yield some direct responses to temperature, but for the most part, temperature will likely elicit an indirect effect on plant species and communities at this site. Temperature is only one of many environmental variables projected to change with global warming (Christensen et al. 2007), and there are many ways it can interact with the abiotic and biotic components of a habitat. Our ability to predict responses of tundra vegetation to climate change requires a consideration of multiple environmental factors and an understanding of ecosystem-level responses.

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